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Boreal Hepaticae, a Manual of the Liverworts of Minnesota and Adjacent Regions[1]

III. Phytogeography[2]

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Bryophytes are able to survive in small niches or "pockets," because their size is so small that their distribution is, within limits, largely a factor of the microenvironment (see, for instance, the papers by Schade, 1917, and Clausen, 1952). For this reason, we may expect Hepaticae (and mosses) to persist in small pockets where a suitable microenvironment persists, long after the general climate of the region has become very definitely "inimical." It would appear that, especially in the case of the "boreal" relicts, the bryophytes can persist for a much longer period than most of the larger vascular plants which are more restricted by the macroenvironment. The diminutive bryophytes, therefore, potentially offer a better clue to the solution of phytogeographical problems than do many vascular plants. This potentiality has not been realized to any extent. This paper will attempt to show that: 1) the Hepaticae (and mosses) agree with the vascular plants in showing very definite, sharply circumscribed patterns of distribution, as already stressed by Müller (1912-1916), Herzog (1926), and Steere (1937); 2) some Hepaticae have a suggestively disjunct range; 3) these latter species may give us a clue as to the Pleistocene and Recent history of the vegetation of the Upper Midwest, especially of the Great Lakes region. The general features of the vegetational history of the area have already been briefly sketched (Schuster, 1957). (See also Butters and Abbe, 1953, for an excellent discussion of the northeastern portion of the area.)

The majority of species of Hepaticae exhibit a relatively narrow distribution, usually restricted to one or a few vegetational zones. A few species

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[2] Two previous sections (taxonomy, ecology) of this work have appeared in THE AMERICAN MIDLAND NATURALIST 49(2):i-v, 257-684; 57(1):203-256; 57(2)257-299. This is the terminal section; it contains the references for the last two sections.

(among them *Marchantia polymorpha, Riccardia pinguis, Scapania nemorosa, Conocephalum conicum*) show such very broad latitudinal ranges that they are scarcely significant for phytogeographical study on a narrowly regional basis. A minority of species exhibit a distribution that is, at first glance, disturbing, since it consists not of a continuous areal, but of a dissected one. This latter type of distribution pattern is particularly interesting because it is usually the result of a reduction in the range of a species, hence may reflect past changes that have modified the vegetation in immediately preceding geological periods. In this section an effort will be made to deal with this historical factor.

Several basic axioms must be recognized. First, it is obvious that the species with a wide distribution north of the boundary to which the Pleistocene glaciers advanced, acquired their present distribution largely or exclusively as a result of postglacial advance from the south or from enclaves, or pockets, which the glacial lobes did not traverse.* This northward distribution was often not a direct northward movement, but frequently involved rapid migration in an east-west line on the recently freed, bare substrates along the retreating ice fronts. The species showing a wide postglacial dispersion toward the north are largely aggressive species (like *Marchantia polymorpha* and *Riccardia pinguis*) whose ubiquitous occurrence and ability to undergo ecesis on a wide variety of substrates stand in sharp contrast to another group of species, with limited distribution. Widely dispersed species are well-known to be genetically complex, with development of greatly different genotypes.

* The possibility must also be considered that postglacial dispersal may also have occurred in part from pockets lying far to the north of the area under discussion. For example, note the existing range of *Clevea hyalina* (Fig. 75) and its partial correlation with lack of continental glaciation, both to the south and in the *high Arctic*.

Fig. 24.—Coniferous Forest Biome. Mature *Thuja occidentalis*, Encampment R.; with *Frullania asagrayana, Radula complanata*, etc., on bark. (See *Frullania-Radula-Porella* Associule; Part II, p. 276.)

Fig. 25.—Coniferous Forest Biome. Shaded, humid rock walls, Encampment R.; with *Porella platyphylloidea, Radula complanata, Lejeunea cavifolia;* on bark of adjacent tree the same species, accompanied by *Frullania bolanderi, F. eboracensis* and *Neckera pennata.* (See *Frullania-Radula-Porella* Associule; Part II, pp. 266, 276.)

Second, those species with a limited distribution pattern (such as *Asterella ludwigii,* the *Mannia pilosa-sibirica* complex, *Clevea hyalina*) are obviously unable to invade more than one or a few limited and related types of environments; they are mostly "pioneers" and often "calciphiles." These species, possibly because of their strict edaphic "demands" are not able to move as rapidly, and probably not able to compete as freely (indicated by their pioneer nature) as the more ubiquitous types. For the student of phytogeography these species, then, are the more "critical" ones. They will be dealt with in detail in this section and the ranges of the various species will be indicated on the succeeding maps. In essence, therefore, we deal with two groups of species: those whose existing distribution is wide, and reflects their great tolerance to climatic conditions; and a smaller group of species whose distribution is definitely circumscribed, often existing today in small pockets where proper edaphic conditions occur, but in areas where the macroclimate may not be at all favorable. The persistence of these latter species has implications that are of some interest to the botanist at large.

Before we deal with this latter group of species, a brief outline of the zonal distribution of the more widespread species is given as a background for the discussion of the species with a restricted distribution pattern. It should first be emphasized, however, that no absolute distinction is uniformly possible between the so-called "critical" species, i.e., those with a discontinuous range, and the species showing no major discontinuities in range. Furthermore, some of the evident discontinuity in range may actually be an artifact due to discontinuity in collecting. In general, the species showing an east-west discontinuity are more sharply defined as a group, since the discontinuity is usually the result of complete or partial extinction consequent to Pleistocene glaciation. The species with a north-south discontinuity are more difficult to deal with

Fig. 26.—Coniferous Forest Biome. Temperance R. Damp rock walls; various members of the *Scapania-Lophozia* Associule (in moist or shaded sites) and *Lophozia barbata-Lophocolea minor* Associule (on dry rock walls). (See Part II, pp. 267, 269.)

systematically. Among these is the large group of so-called arctic-alpine species which have disjunct outliers in the Lake Superior region. The disjunct outliers give the general impression of being relict stands, left behind when the species "migrated" northward in the immediate glacial period. The north-south disjuncts, as a consequence, are less striking. Collecting in the area between the north shore of Lake Superior and Hudson Bay may, furthermore, demonstrate that this disjunction is much less than the existing data suggest.

SPECIES NOT SHOWING A DISJUNCT DISTRIBUTION PATTERN IN NORTH AMERICA (CONTINUOUS AREAL)

The vast majority of our species show a zonal distribution that corresponds well with the distribution pattern of the higher plants. This close correspondence appears because the macroclimate (rainfall, temperature, length of growing season, etc.) conditioning the distribution of the higher plants is also a limiting factor in the distribution of the bryophytes. This is so evident that further note of it would be belaboring the obvious. As with the vascular plants, there is a distribution pattern following largely the four zones represented in the state (for a map of these zones see Schuster, 1957, p. 259). However, the floristic relationships of the Hepaticae in each of these four zones often show some peculiarities worthy of further mention. Some of the typical species of each of the four zones and associated vascular plants are briefly outlined.

1. *The Prairie Biome.*—The prairie area is virtually devoid of Hepaticae, as is to be expected, because of the high moisture requirements of most Hepaticae. However, the decidedly xerothermophytic species, *Mannia fragrans*,

has a distribution pattern in Minnesota that nearly, if not quite, follows the distribution of the prairie (Fig. 40).* Elsewhere, this species is widely distributed on warm, insolated ledges. It occurs under such conditions on the ledges along the St. Croix River, on the Wisconsin side of Taylors Falls. Except for this species, other Hepaticae of this area belong almost exclusively to the Suborder Ricciinae.

HEPATICAE	TYPICAL VASCULAR PLANTS
Mannia fragrans (Fig. 40)	*Equisetum kansanum*
Riccia dictyospora (Fig. 41)	*Zigadenus* sp.
R. fluitans	*Petalostemum* sp.
R. hirta	*Viola pedatifida*
R. sorocarpa	*Geum triflorum*
R. trichocarpa (Fig. 42)	*Bouteloua* sp.
R. beyrichiana	*Stipa* sp.
R. austinii (Fig. 43)	*Opuntia humifusa*
Ricciocarpus natans	

Of these species, *Riccia fluitans* and *Ricciocarpus natans* show a wide distribution elsewhere in the state (except for the northeastern quarter); in the prairie they are limited to streams and temporary or permanent pools. *Riccia trichocarpa* (Fig. 42) and a few other species of *Riccia* possibly represent dis-

* The species is common eastward on exposed ledges and sunny hillsides; however, these sites are usually warm, south-facing, xeric sites. In much of Europe the species is also a xerothermophyte, but there shows a similar, puzzling distribution in high alpine sites ("*Grimaldia controversa*" Meylan). It is evidently of amphizonal distribution. A completely disjunct occurrence in the Scoresby Sound Region of eastern Greenland also should be noted.

Fig. 27.—Coniferous Forest Biome. Turbulent and deeply cut gorge of Temperance R. On damp rocks various calciphilous facies of the *Scapania-Lophozia* Associule (*Leiocolea-Preissia-Scapania* Facies) and *Lophozia heterocolpa-Blepharostoma-Tritomaria scitula-Odontoschisma macounii* Associule (*Lophozia heterocolpa-Blepharostoma* Facies). (See Part II, pp. 268, 272.)

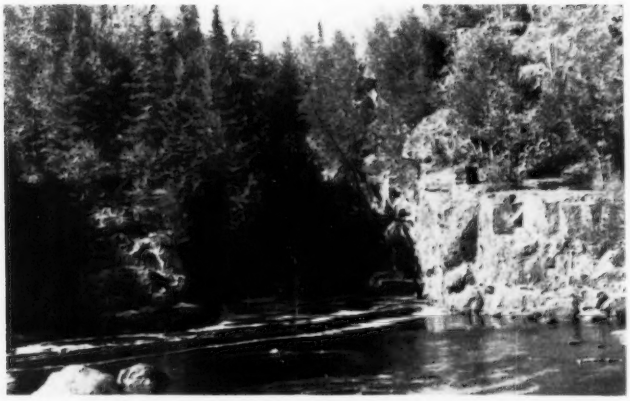


Fig. 28..—Coniferous Forest Biome. Gorge of Temperance R., facing west. On the deeply shaded north-facing ravine wall various phases of the *Scapania-Lophozia* community complex; the insolated south-facing wall nearly free of Hepaticae.

junct elements of southern distribution that reach their northernmost stations within the southern quarter of the state. Elsewhere, these are not confined to prairie regions. Probably none of the above species is limited to strict prairie conditions (e.g., to the flat, relatively dry meadowlands); the species all occur near or adjacent to postclimax forests extending up the river valleys into the prairie region.

2. *The Deciduous Forest Biome.*—In the maple-basswood climax, as well as in the floodplain disclimaxes, occur a series of characteristic Hepaticae, among them the following:

HEPATICAE	TYPICAL VASCULAR PLANTS
Mannia rupestris (Fig. 44)	*Acer saccharum*
Reboulia hemisphaerica (Fig. 45)	*Tilia heterophylla*
Solenostoma crenulatum	*Trillium gleasoni*
Diplophyllum apiculatum (Fig. 46)*	*Uvularia grandiflora*
Metzgeria conjugata	*Hydrophyllum virginianum*
Frullania inflata (Fig. 47)	
F. riparia	
Riccia crystallina	
R. frostii	
Phaeoceros laevis	

A number of other species are "shared" with the Coniferous Forest Biome, among them: *Lophocolea minor, L. heterophylla, Chiloscyphus pallescens, Scapania nemorosa, Plagiochila asplenioides, Ptilidium pulcherrimum, Radula complanata, Frullania eboracensis,* etc.

The species showing the above distribution pattern occur (in our region)

* The report by Wynne and Steere (1943), from the east coast of Hudson Bay (though accepted by Schuster, 1950) is omitted since it seems very improbable that this is based on a correct identification.

largely in an area with 25-32 inches rainfall and with a growing season of 125-160 days. These species, in general, lack noteworthy distributional anomalies. However, *Diplophyllum apiculatum* appears to have a broadly Appalachian distribution, with relict stations in the Lake Superior area. The range closely parallels that of the broadly Appalachian species *Tsuga canadensis*. The Lake Superior population very possibly was derived in recent times from a Pleistocene population in the driftless area.

3. *The Coniferous Forest Biome.*—The *Abies-Picea* climax, as well as the seral stages preceding it, are rich in Hepaticae (compared with the previous two biomes). Typical species include the following:

HEPATICAE

Lophozia ventricosa
L. ascendens (Fig. 48)
L. porphyroleuca
L. grandiretis (Fig. 53)
L. barbata
L. longidens
L. marchica
Cephalozia pleniceps
C. leucantha (Fig. 49)
C. lacinulata (Fig. 29)
C. loitlesbergeri (Fig. 50)
Cephaloziella elachista
Scapania glaucocephala (Fig. 51)
S. subalpina
S. apiculata
S. irrigua
S. paludicola
Moerckia hibernica
Anastrophyllum hellerianum
A. michauxii (Fig. 29)
Frullania selwyniana
F. oakesiana (Fig. 53)
Mylia anomala

TYPICAL VASCULAR PLANTS

Lycopodium annotinum
L. obscurum
Abies balsamea
Picea mariana
P. rubra
Juniperus communis
Thuja occidentalis (Fig. 24)
Linnaea borealis
Chiogenes hispidula

Species showing this distribution pattern occur largely in the area with 28-32 inches of rainfall and with a growing season of less than 120 days (to a minimum of 95-100 days in our region). The relatively cool temperatures together with the adequate rainfall result in a high P/E ratio. Therefore the moisture efficiency is much higher than in the Deciduous Forest Biome, where locally the warmer average temperatures result in a much higher evaporation rate. This factor in combination with a rainfall that is no greater and often somewhat less, results in a much less favorable P/E ratio. The very low incidence of species in the Deciduous Forest Biome, compared with the extremely high incidence in the Coniferous Forest Biome, appears to be very largely a consequence of this ratio.

The species of this group are, in some respects, a rather heterogeneous assemblage as is clear from a comparison of Figs. 48-53. Four general types of subarctic species are distinguishable: 1) Those essentially transcontinental in the spruce-fir zone, but never occurring southward in the Southern Appalachians (*Cephalozia leucantha, C. macounii, Scapania glaucocephala, S. apiculata* [Figs. 49, 51, 52]; clearly allied but more "Hudsonian" in range is *Lophozia grandiretis*, Fig. 53); 2) species restricted to the eastern half of the spruce-fir zone, but never occurring southward into the Southern Appalachians (*Lophozia ascendens, Cephalozia lacinulata* and *C. loitlesbergeri*, Figs. 29,

48, 50); 3) species restricted to the eastern half of the spruce-fir zone, occurring as disjuncts at high elevations in the similar zone in the Southern Appalachians (*Frullania oakesiana*, Fig. 53); 4) species transcontinental in the spruce-fir zone, and recurring as disjuncts at high elevations in the spruce-fir zone of the Southern Appalachians (*Lophozia incisa*, *Anastrophyllum michauxii* and *Calypogeia suecica* are good examples; these are not mapped). The last two groups of species are, in general, less strictly subarctic. The first group, in contrast, includes such species as *Lophozia grandiretis* which are apparently almost restricted to the narrow ecotone between taiga and tundra.

4. *The Tundra Biome.*—As was developed in detail elsewhere (Schuster, 1957, p. 261), there is a very restricted area adjacent to Lake Superior which supports a vegetation so rich in arctic-alpine elements that it should be designated as a "Tundra Strip." The following regional Hepaticae, Tracheophytes and Lichens are characteristic of this narrow zone:

HEPATICAE

Mannia pilosa (Fig. 59)
Lophozia kunzeana (Fig. 54)
L. quadriloba (Fig. 55)
L. alpestris
L. obtusa (Fig. 56)
L. gillmani (Fig. 62)
L. heterocolpa
L. wenzelii s. lat. (Fig. 66)
L. hatcheri (Fig. 70)
L. lycopodioides
L. schultzii (Fig. 72)
Scapania degenii (Fig. 57)
S. cuspiduligera (Fig. 60)
S. gymnostomophila (Fig. 61)
S. buchii (Fig. 73)
Asterella ludwigii (Fig. 58)
Cephaloziella subdentata (Fig. 63)
C. arctica
Anthelia juratzkana (Fig. 64)
Odontoschisma elongatum (Fig. 65)
O. macounii (Fig. 68)
Anastrophyllum saxicolus (Fig. 67)
Tritomaria scitula (Fig. 69)
Marsupella sparsifolia (Fig. 71)
Solenostoma schiffneri (Fig. 74)
S. cordifolium

TYPICAL VASCULAR PLANTS

Lycopodium selago
Selaginella selaginoides (Fig. 31)
Empetrum nigrum
E. atropurpureum
Sagina nodosa
Primula mistassinica
Pinguicula vulgaris
Vaccinium vitis-idaea
Euphrasia hudsonica
Saxifraga aizoon var. *neogaea*
Scirpus cespitosus (Figs. 30, 33-34)
Poa alpina

TYPICAL LICHENS

(after Thomson, 1954)

Alectoria altaica
Caloplaca stillicidiorum
Cetraria hepatizon
Cladonia coccifera
C. cornuta
C. glauca
Lecanora tristiuscula
Lecidea flavocaerulescens
L. latypizodes
L. lithophila
L. tesselata
Physcia dubia
Rhizocarpon disporum
R. geographicum
Usnea laricina

If this list of Hepaticae is examined, it will be evident that none of the species generally considered as strictly arctic (such as *Lophozia binsteadii*, *Marsupella arctica*, *Scapania hyperborea* [Fig. 57], *S. kaurini*, and *S. simmonsii*) occur in the local attenuated version of the Tundra.

The distribution of *Mannia pilosa* in the deciduous forest region of Iowa and Minnesota is highly disjunct (see p. 313).

Lophozia wenzelii has been generally regarded in recent years as including *L. confertifolia* Schiffn. and *L. groenlandica* (Nees). However, the reports

Fig. 29.—Coniferous Forest Biome. Gorge of Encampment R. Decaying shaded log, lying under Balsam Fir; *Cephalozia-Riccardia* Facies of the *Nowellia-Jamesoniella* Associule (see Part II, p. 277). *Riccardia latifrons* accompanied by *Cephalozia catenulata, C. lacinulata, C. macounii, Nowellia curvifolia, Anastrophyllum michauxii, A. hellerianum, Odontoschisma denudatum* and *Jamesoniella.* (See Part I, p. 504, 506.)

Fig. 30.—Tundra Biome, the "Tundra Strip." Rock pool community of the Susie Islands; *Scirpus cespitosus* tussocks, forming matrix for ecesis of *Selaginella selaginoides-Scapania degenii-S. irrigua-Odontoschisma macounii Associule.* (See Part II, p. 262.)

Fig. 31.—Tundra Biome, the "Tundra Strip." Rock pool community of the Susie Islands; *Selaginella selaginoides*, with strobili, at bases of *Scirpus cespitosus* tussocks. (See Part II, p. 262, and Figs. 30, 32.)

of the former (crosses on the map, Fig. 66) are at least partly referable to the mod. *densifolia* of *L. ventricosa* (and/or *L. silvicola*). However, *L. groenlandica* appears to be a good species, having biconcentric oil-bodies of the *L. silvicola* type whereas *L. wenzelii* has oil-bodies of the *L. ventricosa* type. At least part of the *L. wenzelii* reported from the Susie Islands in Part I of this work represents *L. groenlandica* (dots on map, Fig. 66) rather than *L. wenzelii* s. str. (open rings on map).

Of the European species listed as arctic species, Müller (1916) distinguishes four groups, as follows:

1. Species occurring southward only as far as the Scandinavian glaciers (in Europe); e.g., south about to the southern limit of *Diapensia lapponica*. Two Hepaticae are listed with this relatively high arctic distribution pattern: *Lophozia schultzii* (Fig. 72) and *Cephalozia macounii* (Fig. 49). In 1951 Müller modified his list of species to include such local ones as *Lophozia schultzii* (*L. rutheana*), and *Mannia sibirica* (Fig. 59), as well as a group that has been found only north of the Lake Superior region, among them: *Lophozia binsteadii, Marsupella arctica, Scapania hyperborea* (Fig. 57), *S. simmonsii,* and *S. spitzbergensis*. The latter is also found in an alpine situation in Maine (Schuster, 1951).

Both *Lophozia schultzii* and *Cephalozia macounii* occur locally. In fact they give the impression of being decidedly less northern in their restriction in North America than implied for Europe by Müller. For instance, *L. schultzii* was reported for western New York by Schuster (1949) from a predominantly deciduous forest area with a growing season of about 160 days. *Cephalozia macounii,* on the other hand, is constantly a wood dweller (Fig. 29); hence, by the very nature of its physiological requirements, it cannot

grow north of subarctic-subalpine regions — a distribution pattern readily evident from its regional distribution (Fig. 49).

2. Species widely distributed in northern Europe, as well as in the high mountains of the Alps, with sporadic and disjunct occurrences in the intermediate "Mittelgebirgen." Among the 15 species listed in this group by Müller a few do not occur locally (*Anthelia julacea, Temnoma setiforme* [*Chandonanthus setiformis*], *Gymnomitrium alpinum, Haplomitrium hookeri, Moerckia blyttii*), but ten of them do:

Anthelia juratzkana (Fig. 64)
Clevea hyalina (Fig. 75)
Asterella ludwigii (Fig. 58)
Solenostoma cordifolium
Anastrophyllum saxicolus (Fig. 67)
Lophozia heterocolpa
L. kunzeana (Fig. 54)
L. obtusa (Fig. 56)
L. wenzelii s. lat. (Fig. 66)
Scapania cuspiduligera (Fig. 60)

3. Arctic species of northern Europe, also occurring in the Alps but absent from the "Mittelgebirgen." Of the 27 species listed, only the following eight species occur regionally.

Scapania gymnostomophila (Fig. 61)
S. apiculata (Fig. 52)
S. massalongoi
Mannia pilosa (Fig. 59)
Lophozia gillmani (Fig. 62)
L. quadriloba (Fig. 55)
Odontoschisma macounii (Fig. 68)
Tritomaria scitula (Fig. 69)

Scapania massalongoi is represented locally by *S. carinthiaca,* which is probably conspecific with *S. massalongoi,* or a sibling species thereof.

In 1951 Müller combined Groups 2 and 3 into a "Nordic-alpine Group," of which *Lophozia kunzeana, L. quadriloba, L. gillmani, L. grandiretis, Odontoschisma macounii, Scapania apiculata, S. carinthiaca, S. degenii, Tri-*

Fig. 32.—A narrow "Tundra Strip" along Lake Superior shore, with good development of Spruce-Fir Biome adjacent. On the shaded shoreline rocks at extreme left, various members of the *Scapania-Lophozia* Associule (chiefly *Lophozia alpestris-Scapania nemorosa* Facies); in center of figure the *Scirpus cespitosus* rock pool community. (See Part II, pp. 262, 267.)

Fig. 33.—Tundra Biome, the "Tundra Strip," on Belle Rose Island. Pioneer xerophytic lichen communities; in the rock crevices *Scirpus cespitosus* and the accompanying *Scapania degenii-irrigua-Odontoschisma macounii* Associule. (See Part II, p. 262.)

tomaria scitula and *Solenostoma schiffneri* have been found locally. Several others, thus far found only in the arctic areas north of the region discussed (or more rarely also in alpine areas), are: *Arnellia fennica, Anastrophyllum reichardtii, Gymnomitrium apiculatum, Hygrobiella laxifolia, Marsupella varians, Nardia breidleri, Peltolepis quadrata, Pleuroclada albescens, Sauteria alpina, Scapania crassiretis.*

4. As a fourth group, Müller would distinguish a larger, more inclusive group of what may be called "low-grade" arctic types, occurring in northern Europe, in the mountains of central Europe, as well as usually in the intermediate regions. These species include most of the *Solenostoma, Lophozia, Cephalozia* and *Scapania* species. Müller would consider this as the matrix from which evolved the holarctic floristic element. These species would today be considered by most students as essentially subarctic-subalpine in distribution. (Figs. 48-52). Müller (1951) also distinguishes a "Nordic Group" (in the broader sense) which corresponds largely with Group 4. This includes the following local species: *Anastrophyllum michauxii, A. hellerianus, Mannia pilosa, Lophozia heterocolpa, L. schultzii, L. capitata, L. obtusa, Odontoschisma elongatum, Scapania cuspiduligera, S. paludosa* and *Anastrophyllum saxicolus.*

Of the 44 species showing an arctic-alpine distribution (i.e., not of strictly arctic distribution) listed by Müller (1916), it is evident that 20 species occur locally. Since the area here covered is very small, this must be considered as a very significant fraction of the species that could be expected. If one adds the other regional species, such as *Scapania degenii* (Fig. 57), *Cephaloziella*

Fig. 34.—Tundra Biome; Belle Rose Island. Same as Fig. 33, showing the initial stages of development of the rock pool communities. (See Part II, p. 262.)

Fig. 35.—Tundra Biome and, above lake shore, Spruce-Fir Biome; Belle Rose Island. On the vertical rock walls in center, the pioneer *Frullania*-Lichen Facies of the *Frullania-Radula-Porella* Associule; in more detail on Fig. 36 (see Part II, p. 266); on the extreme right, the secondary communities over acidic rocks, the *Mylia-Odontoschisma-Sphagnum* Associule (see Part II, p. 272, and also Table 5, p. 274); the quadrats cited in Table 5 were taken near the extreme right of the figure, where two quadrats have been removed.

Fig. 36.—Pioneer, xeric *Frullania*-Lichen Facies (see Part II, p. 266); various crustose lichens, at middle in lower part of figure with *Umbilicaria;* with only traces of *Frullania asagrayana* and a few small grass plants. Close-up of part of rock wall in center of Fig. 35.

subdentata (Fig. 63), *C. arctica, Marsupella sparsifolia* (Fig. 71), *Lophozia grandiretis,* (Fig. 53), *L. hatcheri* (Fig. 70) and *L. lycopodioides* that appear to show a predominantly arctic-alpine distribution, a very real arctic-alpine element becomes evident in our flora. It should be stressed that none of these species can be considered purely arctic in range.

The species of the "'Tundra Strip" listed above occur in a very restricted fashion in Minnesota. In many cases, the entire Lake Superior region "supports" only one or two colonies of some of these species, such as *Anthelia juratzkana* at Pictured Rocks, Michigan; *Anastrophyllum saxicolus* at Pigeon Point, Minn.; *Lophozia wenzelii* s. lat. at Susie Islands, Minn.; *Lophozia quadriloba* at Keweenaw Peninsula, Mich.; *Asterella ludwigii* at Keweenaw Peninsula and Grand Portage region; *Cephaloziella subdentata* at Grand Portage and vicinity, also near Douglas Lake; and *Marsupella sparsifolia* at Porcupine Mts., Michigan. The very localized distribution of many of these species is perhaps nothing more than a result of the very localized restriction of a "fit" environment. In other cases, the pattern of restriction is so great that we are tempted to speak of disjunct species. To what extent the above group of species is to be considered "disjunct" is not clear. It cannot become clarified until the northern edge of Lake Superior, in Ontario, is carefully explored, and the land mass lying between there and James Bay is studied. For the time being, many of these species appear to show a sufficiently restricted distribution so that they are better discussed in the following section.

All of the species here listed occur within a very short distance of the Lake Superior shore. They occur in an area where the growing season is longer, or at least no shorter than in the Coniferous Forest Biome. However,

the moisture-laden lake winds, fog, and the depressing effect of the cold lake waters (lowering the temperature, consequently the evaporation rate), all conspire to produce a much more adequate P/E ratio. The extraordinary abundance of the species of the Coniferous Forest Biome, together with the occurrence of the above tundra types, results in an extremely rich and diversified hepatic flora of these localized niches adjacent to the Lake Superior shore.

Finally, it should be stressed that all of the species treated above, of all four biomes, are clearly members of the holarctic floristic group, with a few possible exceptions, among them: *Riccia austinii* (Fig. 43) and *R. trichocarpa* (Fig. 42). These species show a distribution pattern very analogous to the Mediterranean floral region of the Old World, a distribution that we might characterize as an Austral-Sonoran distribution, in the New World. *R. austinii*, for instance, is at best a vicarious (sibling) species or race derived from a common stock with the European *R. lamellosa*. [In fact, Müller (1940) unites the two species, and has recently been followed in this by McGregor (1955).] *R. trichocarpa* is a species with a previously known distribution from California to Texas, and has just been reported to occur northward to Kansas. Its occurrence in Minnesota is therefore somewhat "disjunct" with the present state of our knowledge. However, further collecting in the prairie regions from Texas northward, will certainly show the species to occur continuously, if sparsely, i.e., to exhibit a "continuous areal distribution."

None of the so-called Atlantic species (considered generally of oceanic origin) occur locally, not even such low-grade oceanic types as *Lejeunea ulicina, L. patens, Calypogeia arguta, Jubula hutchinsiae, Radula tenax*, etc. The very "low-grade" Atlantic species *Calypogeia fissa* has been reported for southeastern Iowa by Conard (1945), who also reported the strictly Atlantic

Fig. 37.—The *Mylia-Odontoschisma-Sphagnum* Associule (see Part II, p. 272) of the Spruce-Fir Biome. The quadrat outlined is Plot 1 in Table 5 (Part II, p. 274).

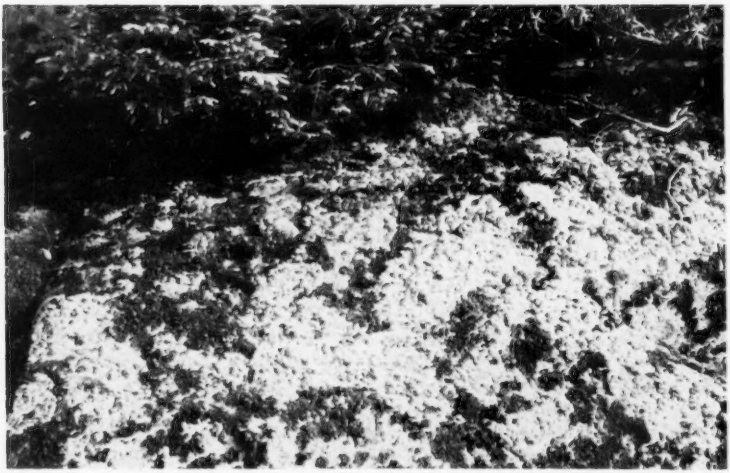


Fig. 38.—Initial, pioneer lichen community below the community in Fig. 37; note early invasion by Spruce and *Ledum groenlandicum* over shallow peat. No invasion by Hepaticae has occurred.

Odontoschisma prostratum from Iowa. The latter, however, is clearly a misdetermination for *Solenostoma crenulatum* var. *gracillimum*.

In summary, therefore, the generalization may be expressed that the species of the area are essentially holarctic in distribution, with the above very few exceptions. Furthermore, the species are all essentially characteristic of continental regions and not of oceanic origin. However, a very few of our species show, in the broadest sense, a disjunct distribution (on an intercontinental basis), among these are:

Lophozia hatcheri (Holarctic area; Japan; Himalaya; again recurring in the southern hemisphere in Patagonia).

Lophozia heterocolpa (Europe; Madeira; Iceland; arctic and subarctic North America; Himalaya).

Mannia rupestris (Japan; eastern temperate North America; boreal and temperate Europe, south to Yugoslavia).

Notothylas orbicularis (Central Europe; temperate eastern North America; Galapagos Islands).

Ptilidium ciliare (Holarctic area; New Zealand; Patagonia).

Trichocolea tomentella (Europe, southeastward to Bulgaria; temperate eastern North America; China and Japan; Himalaya).

SPECIES SHOWING A DISJUNCT DISTRIBUTION PATTERN (DISCONTINUOUS AREAL)

The species treated in this connection are characterized by a distribution pattern that has been restricted in North America as a result of the Pleistocene glaciation. There is a generalized statement regarding the effect of glaciation in Schuster (1957, pp. 207-208). It should be stressed that almost all the regional species with a disjunct distribution fall into one of the two following basic categories: 1) Distribution disjunct in an east-west manner, consequent upon regional extinction during the Pleistocene (Figs. 76-79); 2) Distribution disjunct in an essentially north-south manner, consequent upon the species being forced southward during the glacial period, with postglacial disjunct "pockets" left far to the south of the main body of the present-day distribution. (Figs. 55-57, 66).

In the taxonomic section of this work (Schuster, 1953), the disjunct and isolated distribution of a number of species was stressed, e.g., that of *Scapania degenii, S. carinthiaca, Asterella saccata,* etc. The distribution of these species, taken individually, seems scarcely comprehensible. However, when studied in conjunction with the entire vegetational history of the Middle West, their range in many cases can be clarified. Indeed, their distribution pattern has a direct bearing on our theories regarding the origin of the recent flora of the upper Middle West. For that reason, the problem of distribution of Hepaticae in the entire area peripheral to Lake Superior must be examined in its relationships to the larger problem of plant distribution of the area as a whole.

The vegetational history of the Middle West, and especially of the Great

Fig. 39.—Pioneer lichen community below the community in Fig. 37. Note grasses and *Potentilla tridentata* in exposed crevices at left; *Polytrichum* community on horizontal ledge in upper center. At this point invasion by Hepaticae has not yet begun.

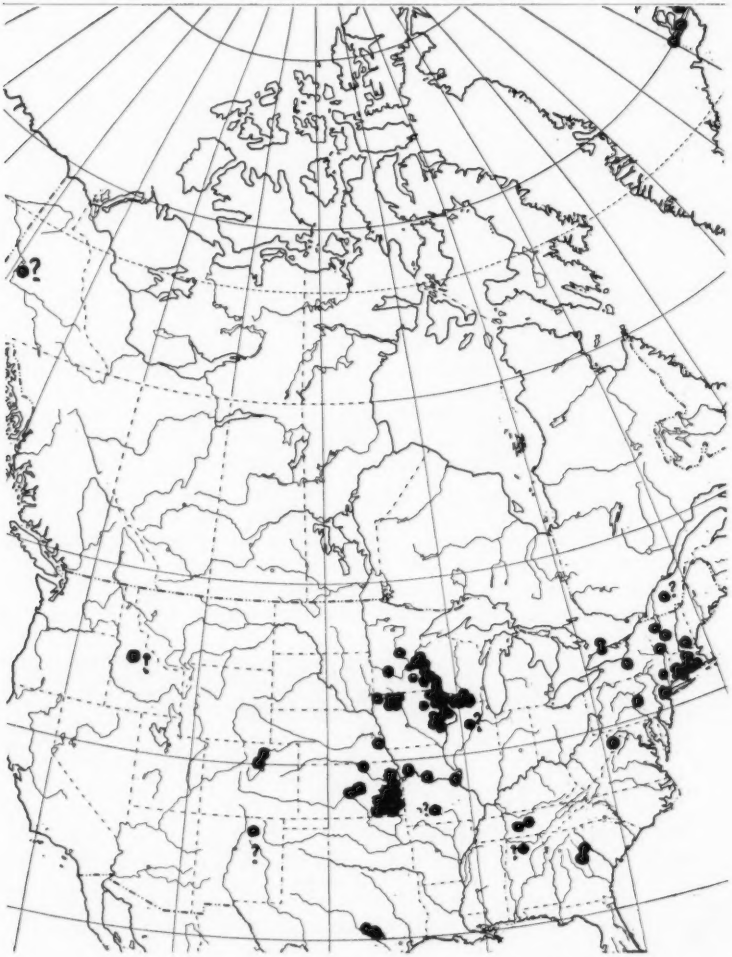


Fig. 40.—Distribution of *Mannia fragrans* in North America.

Lakes region, remains a controversial subject. This is readily apparent when one compares the paper by Fernald (1925), in which the driftless area south of Lake Superior is suggested as a source for the revegetation of the Great Lakes region (subsequent to the last glaciation), with other recent ideas on the subject. Compare, for instance, this theory with that of Fassett (1931) which is in opposition, at least by implication, and with a later paper by Fernald (1935) wherein the driftless area is "discarded" in favor of hypothetical unglaciated areas, or Nunataks, and, lastly, with the

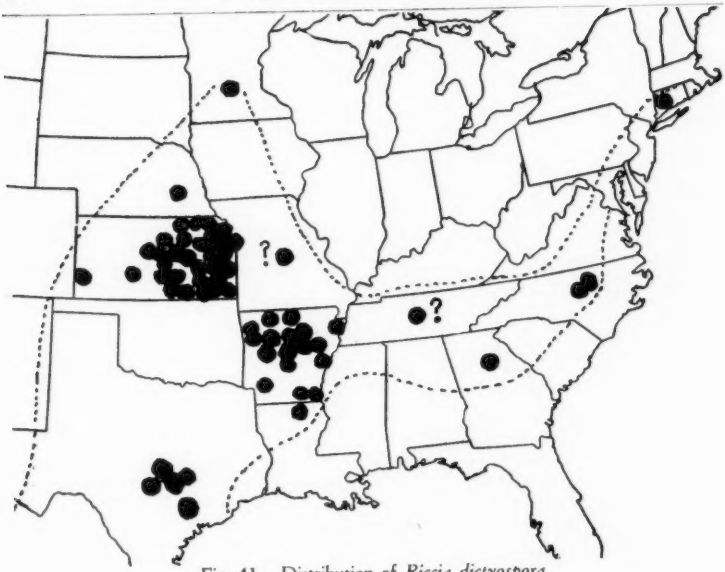


Fig. 41.—Distribution of *Riccia dictyospora*.

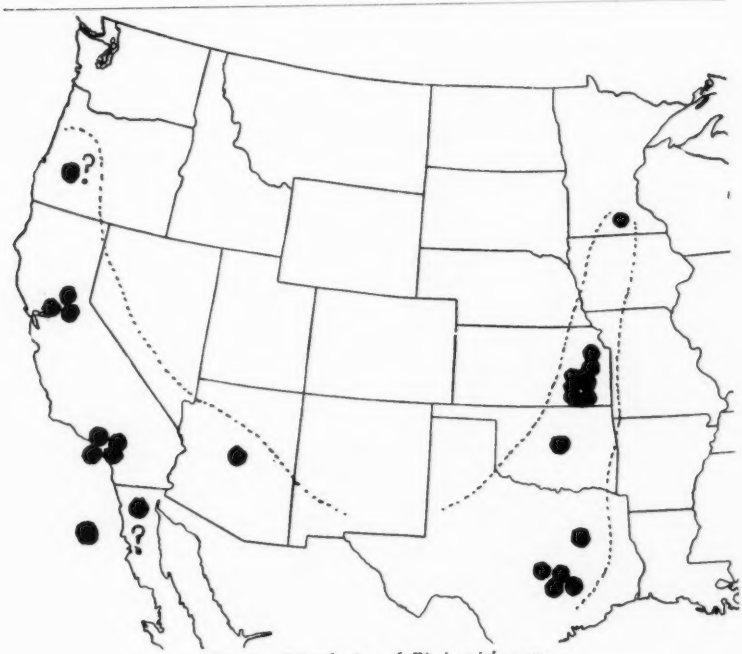
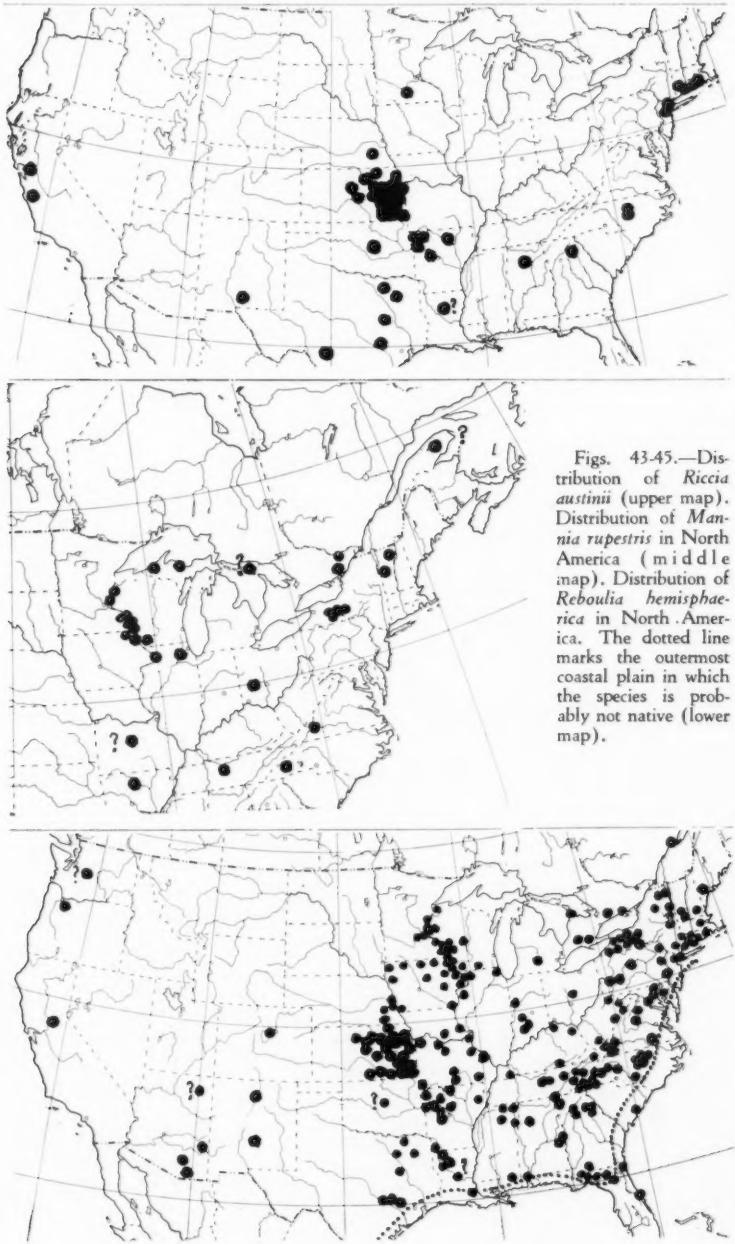
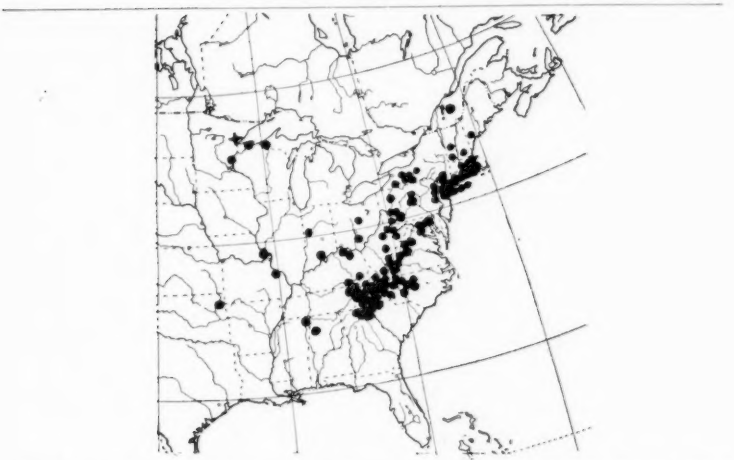
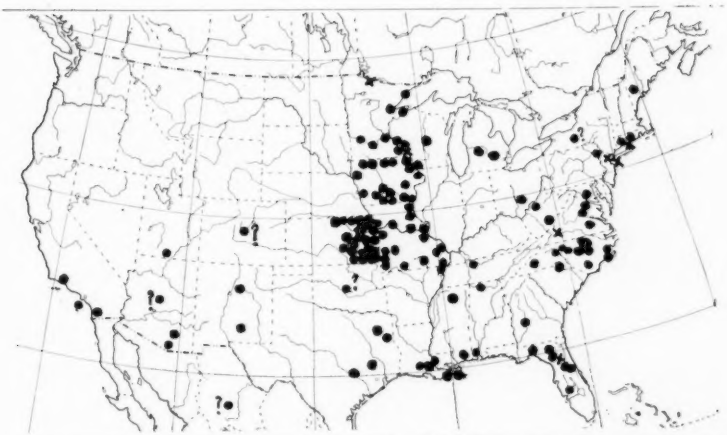


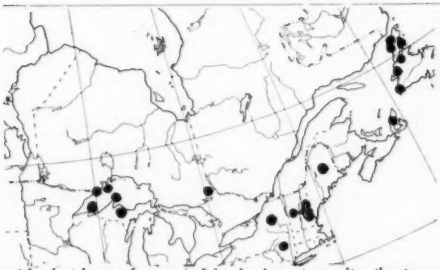
Fig. 42.—Distribution of *Riccia trichocarpa*.



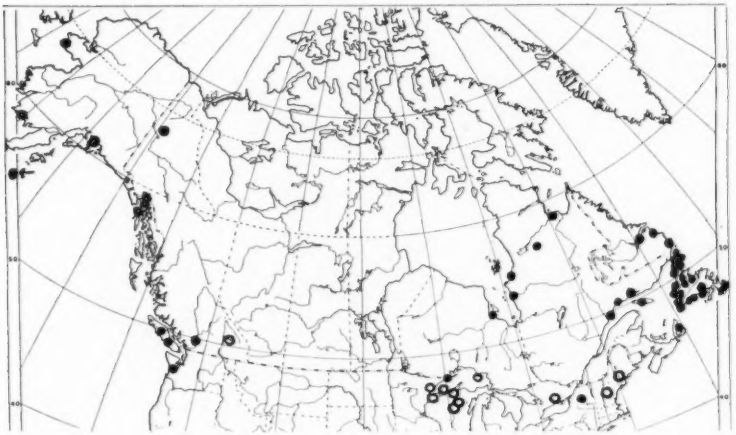
Figs. 43-45.—Distribution of *Riccia austinii* (upper map). Distribution of *Mannia rupestris* in North America (middle map). Distribution of *Reboulia hemisphaerica* in North America. The dotted line marks the outermost coastal plain in which the species is probably not native (lower map).

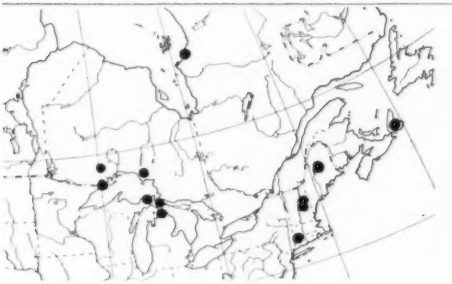




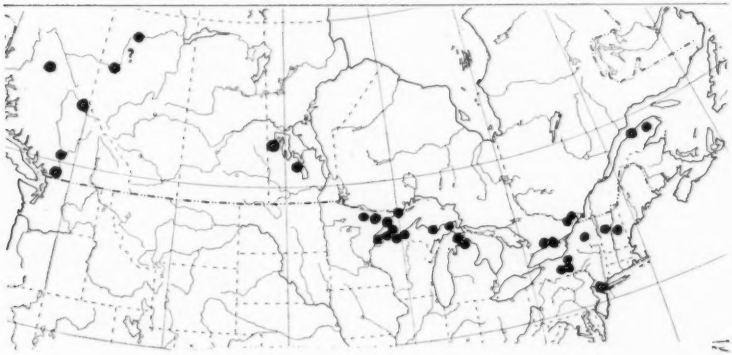


Figs. 46-48.—Distribution of *Diplophyllum apiculatum* (upper map). The cross marks the station for var. *obtusatum*. Range closely parallels that of *Asplenium cryptolepis* (see Map 5, in Fernald, 1933). North American distribution of *Frullania inflata* s. lat (middle map) (incl. *F. catalinae* and *F. mexicana*), dots; and *F. saxicola*, crosses. (Distribution general in areas with deciduous forests.) North American distribution of *Lophozia ascendens* (lower map). Range closely parallels that of *Utricularia geminiscapa* (see Fernald, 1933, Map 6).





Figs. 49-51.—North American distribution (upper map) of *Cephalozia leucantha* (dots) and *Cephalozia macounii* (open rings). North American distribution of *Cephalozia loitlesbergeri* (middle map). North American distribution of *Scapania glaucocephala* (lower map).



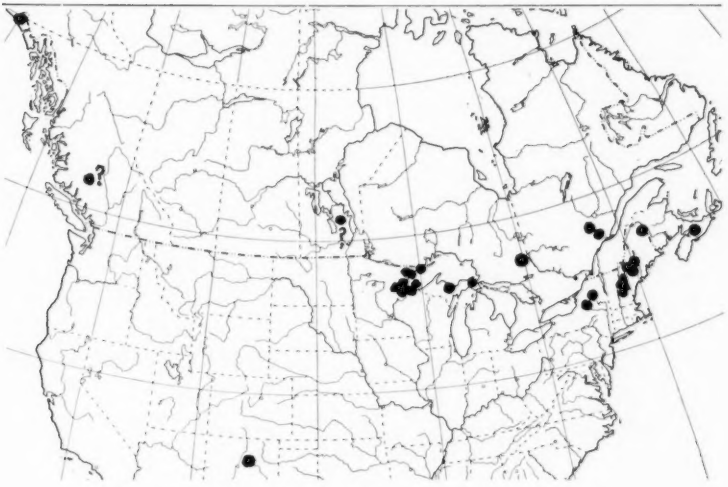


Fig. 52.—North American distribution of *Scapania apiculata*.

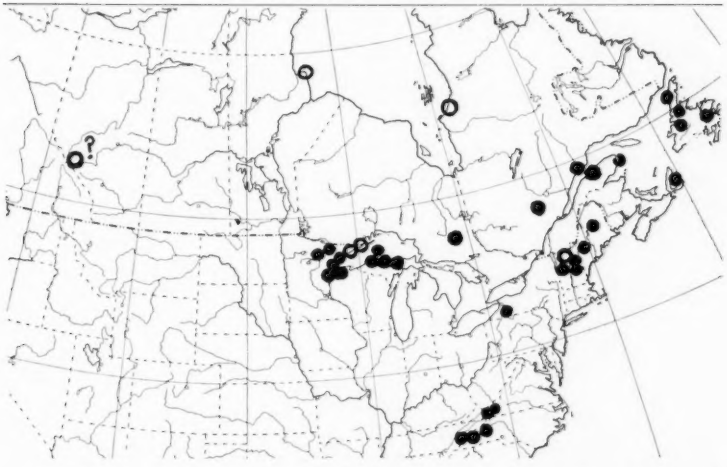


Fig. 53.—North American distribution of *Lophozia grandiretis* (rings), a high subarctic (Hudsonian) species, and *Frullania oakesiana* (dots) a low subarctic-subalpine species (Canadian zone). The range of *Frullania oakesiana* closely parallels that of *Cypripedium reginae* (see Fernald, 1933, Map 2).

paper, almost simultaneously published, by Stebbins (1935) suggesting that migration along the retreating ice fronts may have been a source of revegetation. Butters and Abbe (1953) largely follow Stebbins. Since recent geological evidence (Bergquist, 1937) does not substantiate Fernald's ideas regarding Nunataks in the Great Lakes area, questions remain to be answered as to how some of our "disjuncts" acquired their existing ranges.

A possible answer to some of these problems is attempted in the following pages through a comparison of the distribution patterns of both the bryophytes and tracheophytes. First, the regional restriction of the species will be discussed and vascular species showing a similar regional localization will be mentioned. These species are almost all northern in distribution; therefore, the discussion will deal largely with the problem of relict species of boreal and arctic distribution. Secondly, an integration of these distribution patterns into a number of historically significant types will be attempted. Finally, the conclusions that the writer has reached will be discussed.

REGIONAL RESTRICTION OF NORTHERN SPECIES IN MINNESOTA; WITH A DISCUSSION OF UNDERLYING CAUSES

The essentially arctic or arctic-alpine and "cordilleran" elements present in the vegetation of the area are restricted to two centers: 1) The "driftless area,"

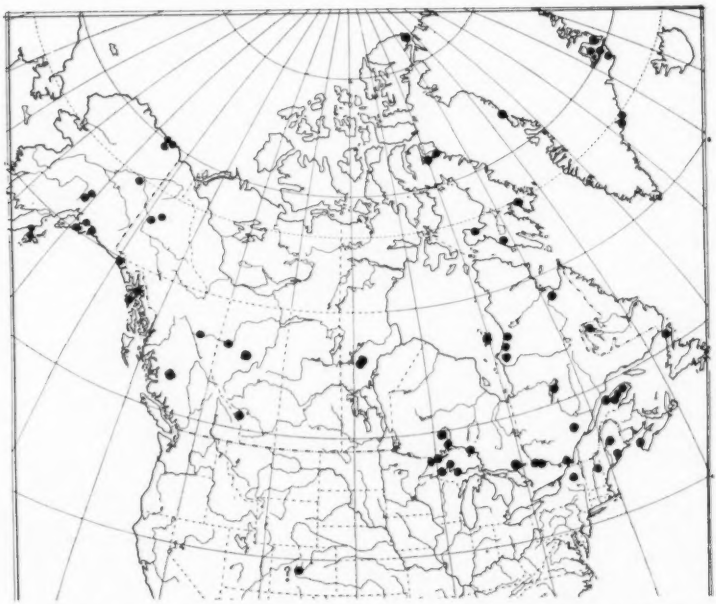


Fig. 54.—North American distribution of *Lophozia kunzeana*. Range similar to that of *Carex alpina* s. lat. (see Fernald, 1933, Map 21).

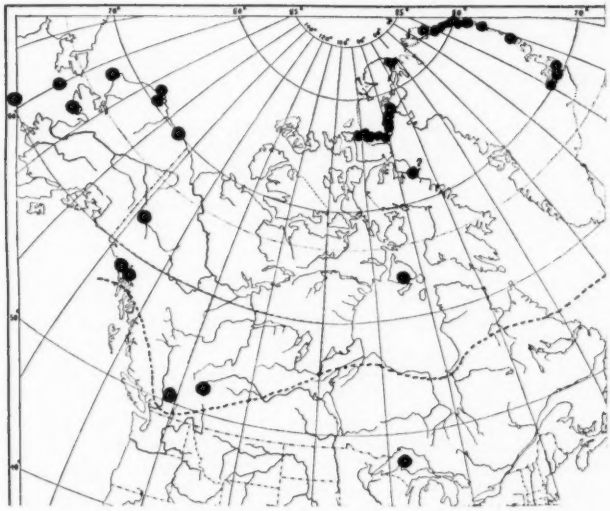


Fig. 55.—North American distribution of *Lophozia quadriloba*. (Dotted line marks southern limit in general range.).

of the region lying east and south of southeastern Minnesota and 2) the periphery of Lake Superior, especially in Cook County. This restriction holds equally well for the vascular plants and for the Hepaticae. There are two basically different factors operating to explain the limitation of northern elements to these two regions: historical events and climatic (and, to a lesser degree, edaphic) factors. Fernald (1925, 1935) attempted to maintain a sharp distinction between arctic-alpine and "cordilleran" species. If the series of maps (Figs. 54-79) is studied, no such distinction is apparent. As is commented on later, the few hepatics for which a "cordilleran" range has been postulated (see, e.g., Steere, 1937, who suggests *Solenostoma schiffneri* as a "cordilleran" species; Fig. 74 wholly fails to support such a belief), prove, on further study, to be essentially arctic-alpine in range. Butters and Abbe (1953) also fail to see any such sharp distinction.

The species of arctic and/or "cordilleran" affinity occurring in or around the periphery of the "driftless area" are found there largely because of historical reasons (see Schuster, 1957, pp. 209-210). They are of extremely disjunct occurrence, often surviving only as isolated populations. During the Wisconsin glaciation these species presumably found a refuge in the "driftless area" which then consisted mostly of coniferous forest encircled by at least a narrow tundra fringe in contact with the advancing ice masses first on one, then on the other side. It has been recently shown that the so-called "driftless" in Minnesota (i.e., west of the Mississippi River) and Iowa was entirely glaciated, although but a single time (Conard, 1940). The "driftless area" lying east of the bluffs on the west side of the Mississippi

could readily have served as a "reservoir" from which the region here treated could have been revegetated. Furthermore, with the gradual retreat of the ice, the high bluffs on the west side of the Mississippi must have been exposed at a very early date. A few of the highest of them may have stood out as restricted "Nunataks." The occurrence at Gwynn's Bluff, of so many "disjunct" elements, plus the occurrence at its crest of a dense stand of *Thuja* (the only stand in the "driftless" of Minnesota) may be more than accidental. Existing climatic conditions (and those of the recent past, especially during the postglacial "climatic optimum") have surely served constantly to restrict the occurrence of such northern species in the "driftless area." In Minnesota, for instance, the so-called "driftless strip" includes the most "temperate" portion of the state, with the mildest winters and the longest growing season. The species of the "driftless," such as *Mannia sibirica, Clevea hyalina, Asterella saccata, Preissia quadrata* all belong to the "light-tolerating" (if not "light-loving") Marchantiales. They normally occur under conditions where they are exposed to direct sunlight for most of the year. However, in the lush and dense forests along the bluffs of the Mississippi River where these species occur, they are largely restricted to extremely shaded, moist sites — an existence under quite aberrant conditions. It appears probable that their inability to spread from these areas is at least in part a consequence of the fact that they exist under such extremely abnormal and suboptimal conditions, that they are reduced to the status of a genetically

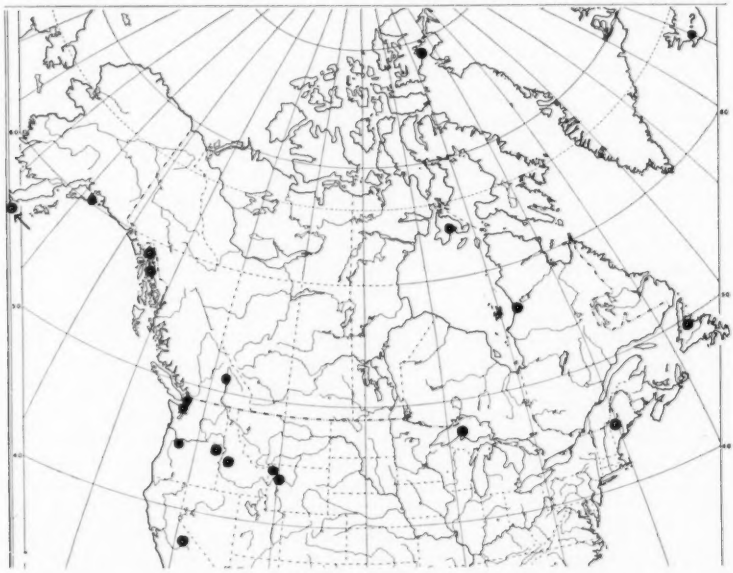


Fig. 56.—North American distribution of *Lophozia obtusa*. (Also on the Aleutian Islands: Unimak, Akutan, Unalaska, and Atka.). Range approaches that of *Saxifraga oppositifolia* (see Fernald, 1933, Map 1), but less extremely Arctic in range.

Fig. 57.—North American distribution of *Scapania degenii* (rings) and *S. hyperborea* (dots). The range of *S. degenii* approaches that of *Scirpus cespitosus* var. *callosus* (see Fernald, 1933, Map 10).

stenotopic fringe-element, not quite eliminated from the vegetation but decidedly unable to compete with the existing vegetation. It is also probable that the existing northern relict species found there today represent but a small remnant of a much more extensive arctic flora that at one time had a foothold there. The presence of these relict species in the "driftless" may be said to be *in spite of*, rather than *because of*, existing or recent climatic conditions. The historical and climatic factors here are obviously working against each other.

The species of arctic and/or "cordilleran" affinity occurring in the immediate vicinity of Lake Superior (i.e., in a hypothetical "Arrowhead Enclave") presumably must occur there today entirely as a consequence of postglacial or late Pleistocene immigration and are now found there largely because of the existence of a narrow zone (influenced very obviously by the cooling effect of the lake) in which essentially tundra conditions persist. In other words, the species along the shore of Lake Superior occur there today partly *because* of the persistence of locally favorable climatic conditions and not in spite of them. These northern species, therefore, are in one

sense not strictly "relict" species at all. Both historical and climatic reasons here operate in concert to make survival of these elements possible.

As will be shown later, there is an organic connection between the northern floristic elements occurring in the "driftless" and those in the lake region. It appears possible, in fact, that at least some of the northern species occurring today in the vicinity of Lake Superior survived the last glaciation in the "driftless area."

These two general areas, and the species that today survive there may now be discussed in some detail.

1. *The "Driftless Area."*—This, in Minnesota, has been traditionally stated to include the southeasternmost part of the state (portions of Winona, Fillmore and Houston counties). (See Schuster, 1957, p. 207). With the absence of extensive glaciation, there has been development of an extremely dissected topography: meandering and mature streams, along the north- and east- facing sides of which there are often high, vertical cliffs, and moist,

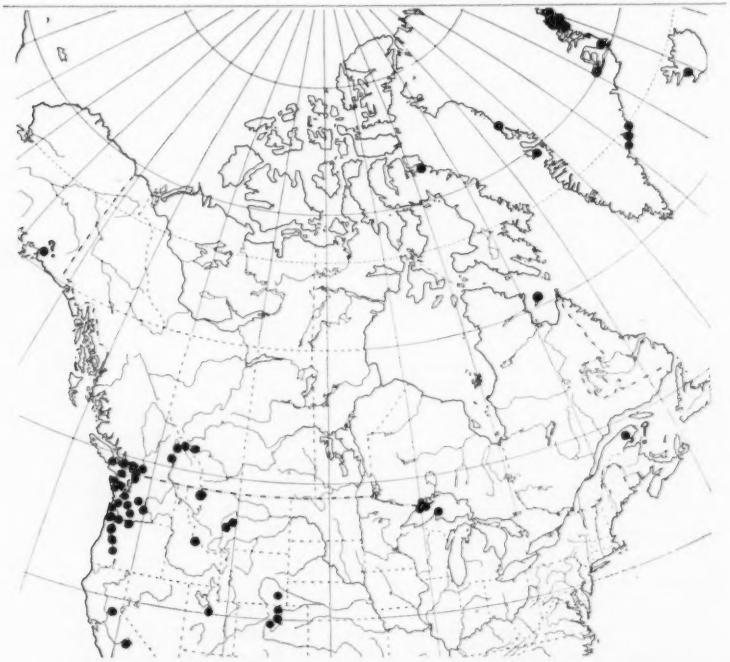


Fig. 58.—Nearctic range of the holarctic *Asterella ludwigii*. Frye and Clark (1937) report the species also from Massachusetts, New York, Missouri, Nebraska, Quebec and the Canary Islands. All of these are old or clearly erroneous reports, with the possible exception of that from Quebec (indicated on the map with a question mark). The range closely approaches that of *Polystichum lonchitis* (see Fernald 1935, Map 3).

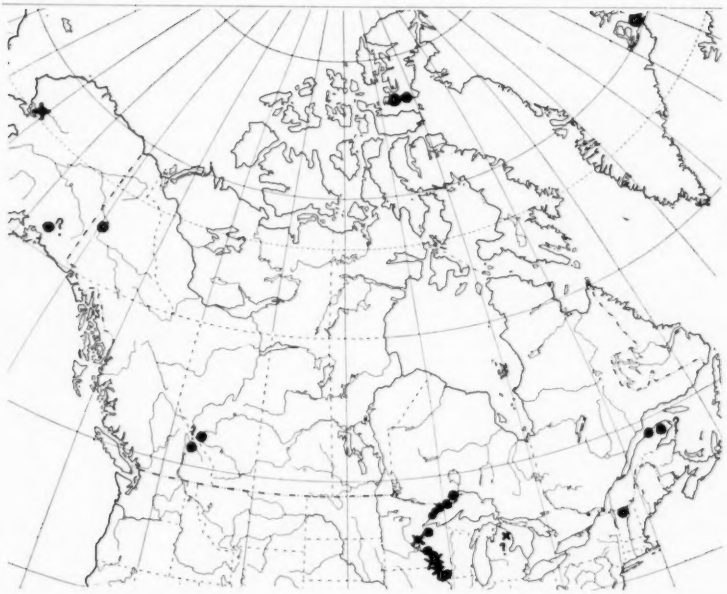


Fig. 59.—North American distribution of *Mannia pilosa* (dots) and *M. sibirica* (crosses). Some of the stations for the former may represent *M. sibirica*. The two taxa are very close and may not prove separable at all times.

shaded talus slopes. It is on these cool, often sheltered cliffs and shaded rock outcrops, that the arctic-alpine and "cordilleran" Hepaticae survive; among them are:

Mannia pilosa (Fig. 59)	Arctic-Alpine and/or Cordilleran
M. sibirica (Fig. 59)	
Clevea hyalina (Fig. 75)	
Asterella saccata (Fig. 76)	
Preissia quadrata	Ubiquitous in the Subarctic-Subalpine
Scapania mucronata	
Ptilidium ciliare	
Lophozia muelleri	
L. incisa	
Tritomaria exsecta	
Plagiochila asplenioides	
Harpanthus scutatus	

In addition, several other elements occur here. There is a "Coastal Pacific Element," represented by the West Coast species, *Frullania bolanderi* (Fig. 77). There are also traces of a southern, xerothermophyte element, represented by *Frullania riparia*, *F. inflata* and *F. saxicola* (Fig. 47), *Reboulia hemisphaerica* (Fig. 45) and *Mannia fragrans* (Fig. 40). The flora of the area has been long known to be highly synthetic, suggesting a diversified origin.

This is also stated by Steere (1937a): "The bryophyte flora of any unglaciated area will contain representatives of at least three main groups: (1) The majority of species are ubiquitous and aggressive ones, many of which have probably migrated into the area in postglacial times. . . . The presence of this large group of very tolerant species tends to obscure the presence of more significant ones; . . . (2) Relic species of the warmer climate which existed before glaciation. . . . (3) Boreal species, which invaded the area as they retreated before an advancing ice-sheet. . . ."

Associated with the northern Hepaticae listed above are (in the general area) such northern vascular species: *Potentilla tridentata, Moneses uniflora, Primula mistassinica, Mertensia paniculata, Sedum roseum, Rhododendron lapponicum,* etc. (See discussion starting p. 319).

Although only four arctic-alpine species can be listed so far from the "driftless," it should be stressed that less than 35 species of Hepaticae occur there. Of these, a number penetrate far northward into the Arctic. Hence the "facies" of the hepatic flora of the region is predominantly northern.

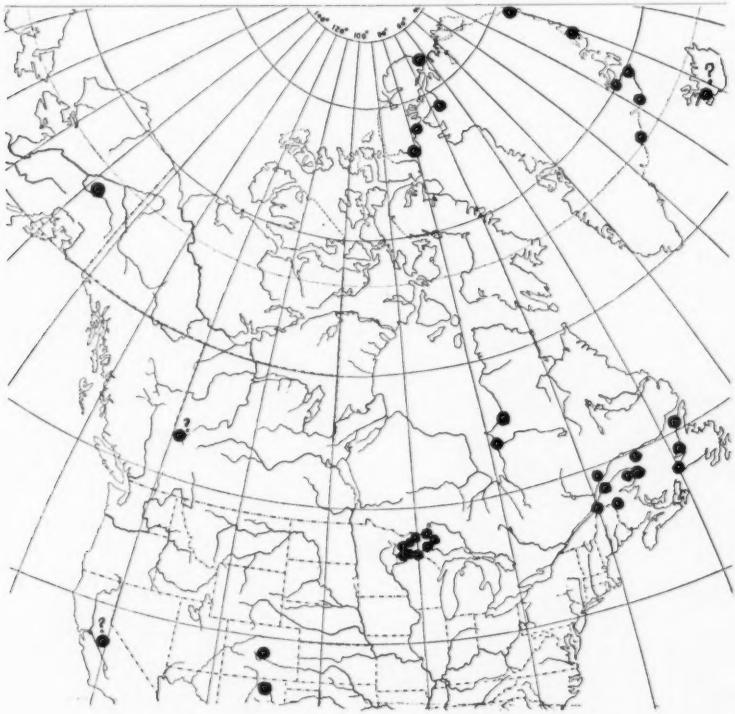


Fig. 60.—North American distribution of *Scapania cuspiduligera.*

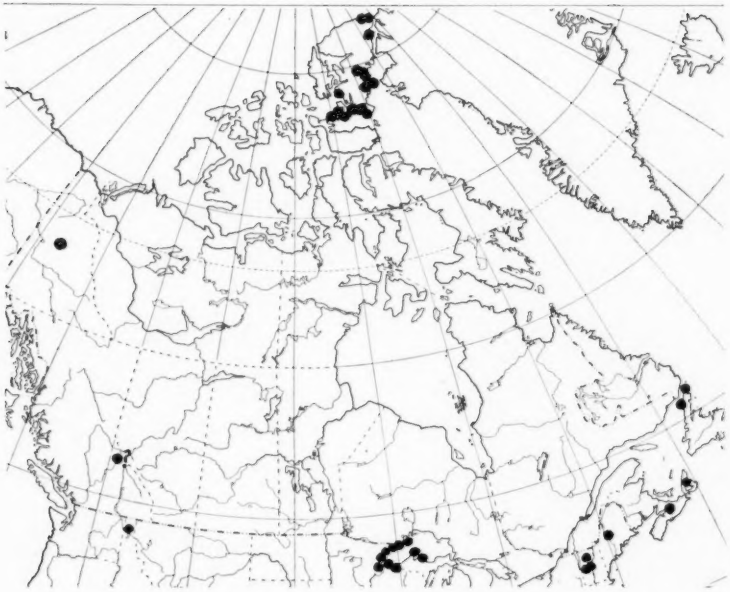


Fig. 61.—North American distribution of *Scapania gymnostomophila*.

2. *The Northeastern Corner of Minnesota.*—By this area is understood the hypothetical "Arrowhead Enclave," the region of borderline lakes and the Pigeon Point area (and the associated Susie Islands to the south). This area possibly was not completely covered by ice *at any one time* during the latter stages of the Wisconsin glaciation (Schuster, 1957, p. 207). The region is much richer in arctic-alpine species. In addition, it contains a large number of more ubiquitous species which occur with nearly equal frequency in both Arctic and Subarctic regions (such as *Tritomaria quinquedentata, Scapania, undulata, Preissia quadrata, Gymnocolea inflata,* etc.).

There are two general types of sites to which the arctic-alpine species of Hepaticae are restricted: one of these supports only slight remnants of an arctic-alpine flora (so will be dealt with last) but in the other site there is a preponderance of arctic-alpine forms. These are discussed below and beginning p. 294.

SITES RESTRICTED TO THE IMMEDIATE VICINITY OF THE LAKE SUPERIOR SHORE

Two basically different types of habitats are included here and treated separately below. The occurrence of the arctic-alpine species is restricted almost exclusively to the less strongly insolated north- and northwest-facing sides of islands or long peninsulas (e.g., the Susie Islands, the Point at Grand Marais, and Pigeon Point); see Figs. 32 and 35. There is, under such conditions, a

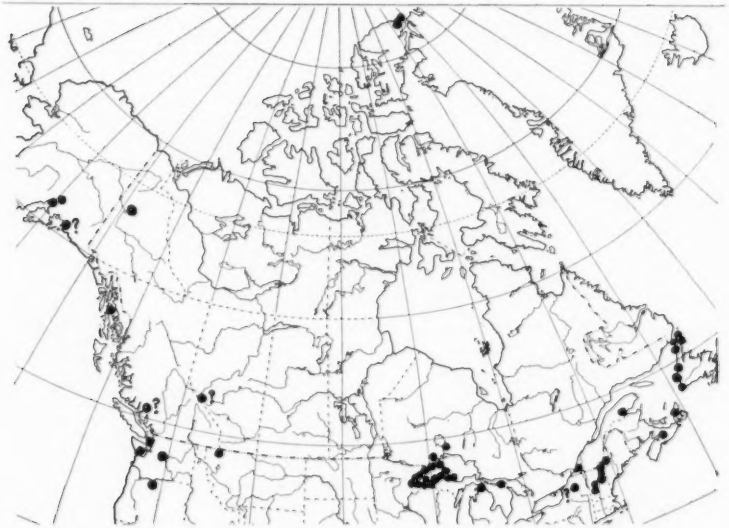


Fig. 62.—North American distribution of *Lophozia gillmani*. Probably ubiquitous in calcareous situations throughout the Canadian Arctic; abundant in N.E. Ellesmere Island (Schuster, 1955).

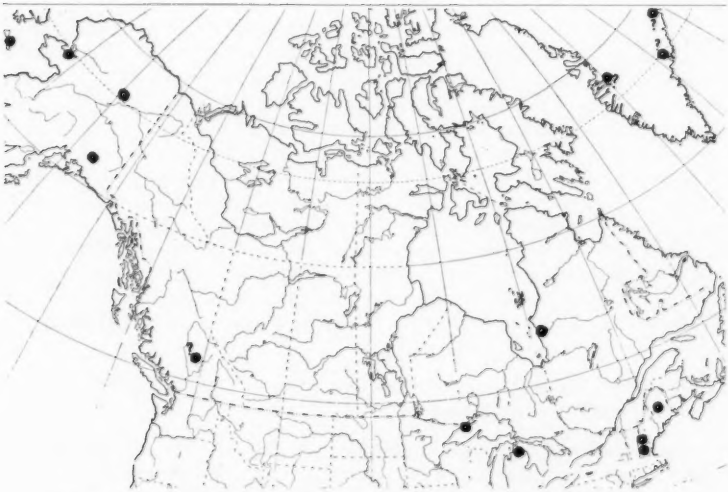


Fig. 63.—North American distribution of *Cephaloziella subdentata* (including *C. spinigera* and *C. spinosa*). The exact localities in Greenland unknown.

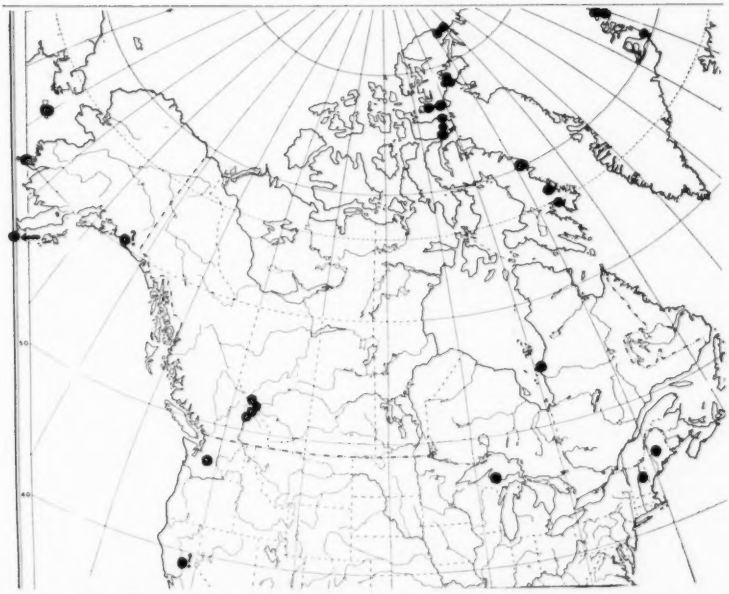


Fig. 64.—North American distribution of *Anthelia juratzkana*. (Several localities in westernmost Alaska, St. Lawrence Island, and the Aleutians not on the map; also in N.E. Ellesmere Island).

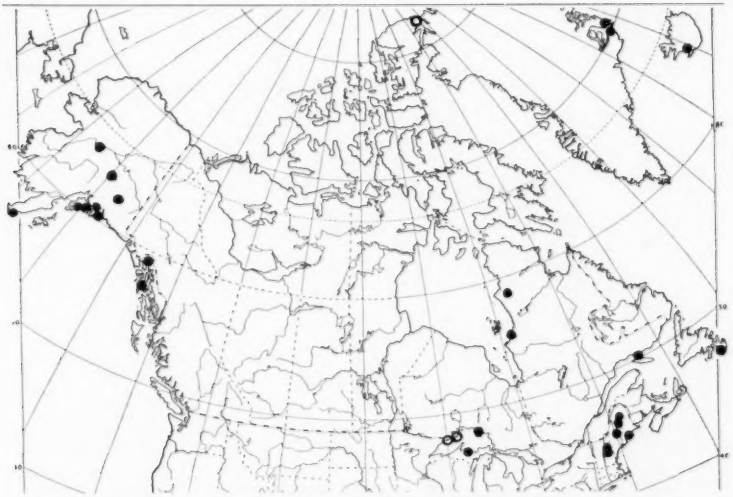


Fig. 65.—North American distribution of *Odontoschisma elongatum* (dots) and *Cryptocolea imbricata* (open rings).

coincidence of environmental extremes that make the succession of less hardy species, and especially of woody forms, a virtual impossibility for these reasons: 1) the cold waters of Lake Superior keep the air cool, even on the hottest days (especially on the north- and northwest-facing slopes, where insolation is a minor factor until late in the day); 2) insolation is extremely low, especially in narrow, deep cuts and on vertical, high cliffs where the sun never hits directly, and therefore the amount of incident solar energy is extremely low; 3) at sites up to 10 feet above the lake level ice-action and wave-action are extremely important in preventing succession. In the deeper cuts in high north-facing rock walls ice may persist until June (while killing frosts may start early in September) leaving microenvironments with a growing season of only some 60-90 days *locally*.

Largely because of the last factor there may exist an edaphically and

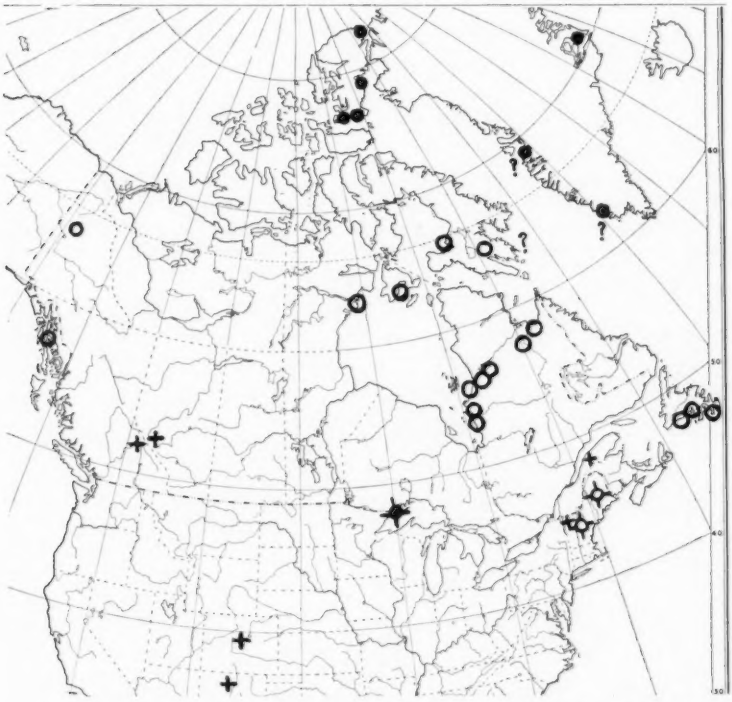


Fig. 66.—North American distribution of *Lophozia wenzelii*, s. lat. (open rings), *L. "confertifolia"* (crosses), *L. groenlandica* (dots). The reports of *L. confertifolia*, supposedly a synonym of *L. wenzelii*, probably are partly referable to *L. ventricosa*. *L. groenlandica*, included in all recent works (including Part I of this work) as a synonym of *L. wenzelii* is evidently distinct from it; at least part of the Minnesota material is referable to it.

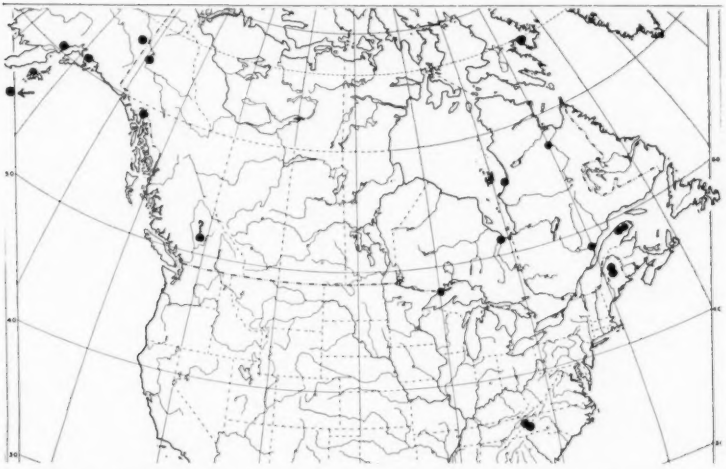


Fig. 67.—North American distribution of *Anastrophyllum saxicolus*. Westernmost report on Attu Island, indicated by dot and arrow, beyond margin of map.

microclimatically controlled "Tundra zone" some 10-30 feet wide and 10-50 feet high (depending on the quantity of direct sunlight); with more insolation the zone may be only 1-12 feet high. To this limited "Tundra zone" belong the following species, which occur in two limited sites:

A. At the edges of rock pools or moist rock crevices and in run-off cuts through horizontal ledges (chiefly on the north-facing sides of islands, at 1-12 feet above the lake level); see Figs. 30-34. The abundant moisture, together with the very nearness of the cold lake waters here counteracts the moderate to high insolation. The pH varies from 7.2 to 5.6.

Here occur the following species:*

Scapania degenii (Fig. 57) *Odontoschisma macounii** (Fig. 68) *Lophozia gillmani** (Fig. 62) *L. latifolia** *L. schultzii* (Fig. 72) *L. kunzeana** (Fig. 54) *Scapania gymnostomophila** (Fig. 61) *Tritomaria scitula* (Fig. 69)	Predominantly Arctic-Alpine
*Ptilidium ciliare** *Tritomaria quinquedentata** (Fig. 81) *Lophozia heterocolpa** *Gymnocolea inflata* *Scapania irrigua* *Cephaloziella rubella* *C. hampeana* *Preissia quadrata**	Ubiquitous in the Subarctic, mostly occurring in the Tundra

* On this, and the immediately succeeding pages, those species occurring northward to northeastern Ellesmere Island (82° 25-32′ N. Lat.), and therefore able to exist under the most severe arctic conditions, are set apart with asterisks.

The first two species (*Scapania degenii* and *O. macounii*) are index species of the arctic-alpine habitats, and are strictly limited to within 25 feet of the lake shore in Minnesota (see Figs. 30-34, also Fig. 21 in Part II).

Also found on moist rocks or rock crevices near the shoreline (but not exclusively around rock pools) are such northern species as *Vaccinium cespitosum, Sagina nodosa, Allium schoenoprasum* var. *sibiricum, Euphrasia hudsonica, Empetrum nigrum* and *E. atropurpureum.*

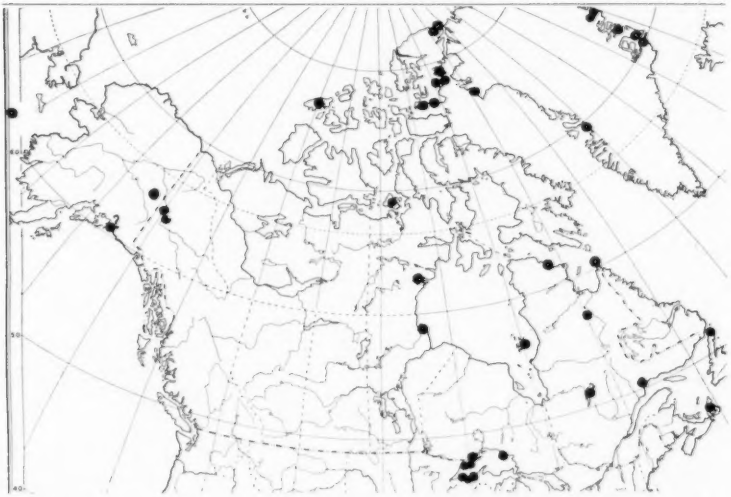


Fig. 68.—North American distribution of *Odontoschisma macounii.* With several other citations from Greenland which could not be accurately localized.

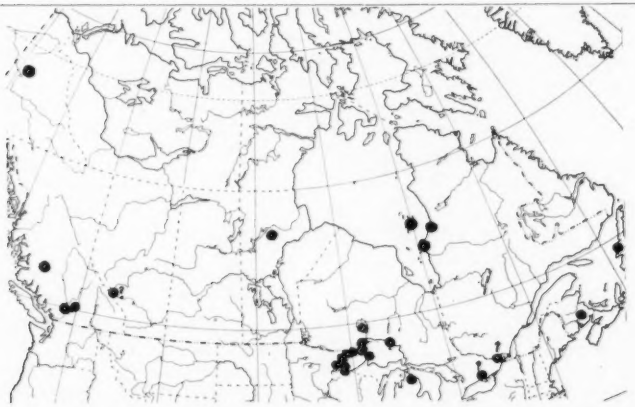


Fig. 69.—North American distribution of *Tritomaria scitula.* The species is replaced in the high Arctic of northern Ellesmere (and presumably elsewhere) by *T. heterophylla* Schuster.

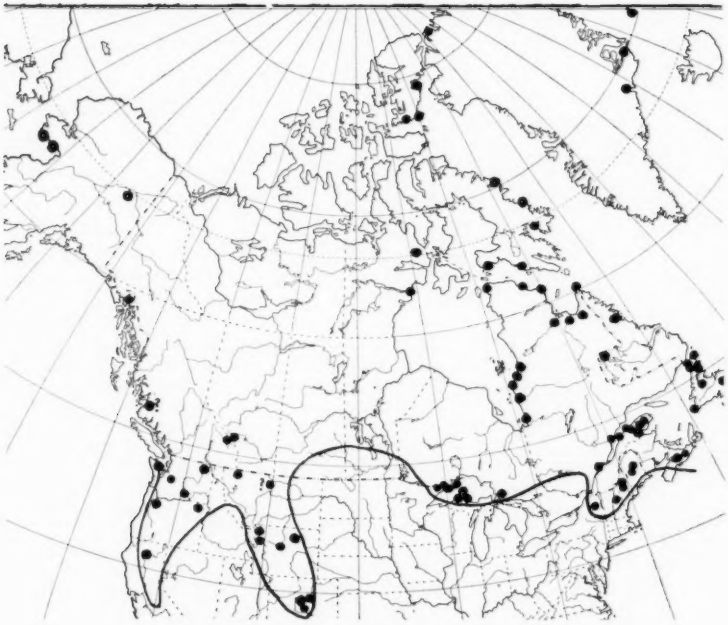


Fig. 70.—North American distribution of *Lophozia hatcheri*.

B. On the vertical cliff walls and on their crests, at elevations of 5-50 feet, but within 0-50 feet (horizontally) of the lake. The extremely low insolation here makes up for the relatively greater distance from the lake shore. The lack of insolation (and relatively high humidity) also make the site very favorable for bryophytes. Three subtypes occur here:

1. Cliff crest communities of secondary species, getting their start usually on *Sphagnum*, occurring at a pH of 3.7-4.5. These species are all secondary species, and come in after a dense *Sphagnum* mat has crowned the cliff crest, often 6-18 inches deep or more. Occurring in areas where the rock is acid or subacid; common vascular species here are *Ledum groenlandicum*, *Vaccinium uliginosum*, *V. oxycoccos*, occasionally *Empetrum atropurpureum* (at less acid extremes); see Fig. 37. Here occur:

Odontoschisma denudatum var. *laevissima* *Cephaloziella subdentata* (Fig. 63) *Lophozia wenzelii* s. lat. (Fig. 66)	Arctic-Alpine
Calypogeia sphagnicola *Mylia anomala* *Cephalozia leucantha* (Fig. 49) *C. loitlesbergeri* (Fig. 50)	Restricted to the Subarctic-Subalpine
Cephalozia pleniceps *Blepharostoma trichophyllum** *Lepidozia reptans* *Lophozia ventricosa* forms *Bazzania trilobata*	Ubiquitous in the Subarctic-Subalpine

2. The vertical cliff wall communities of pioneer species, limited to bare or almost bare rock walls (or their crevices), where the pH is relatively low (*ca.*4.4-5.6). Here occur:

Diplophyllum taxifolium var. *macrosticta*	Arctic-Alpine
Anastrophyllum saxicolus (Fig. 67)	
Solenostoma sphaerocarpum (Fig. 80)	
Lophozia hatcheri (Fig. 70)	
*Anthelia juratzkana** (Fig. 64)	
*Tritomaria quinquedentata** (Fig. 81)	Ubiquitous Subarctic-Subalpine
*Anastrophyllum minutum**	
A. michauxii	
Lepidozia reptans	
Lophozia longidens	

3. The ledge and cliff crest communities of primary to secondary species, getting their start on rock or thin soil or in rock crevices. Their environment has a pH of 7.0 to 5.5; they occur scarcely above the wave action zone. These species are often secondary invaders and usually form dense, peaty masses. Common or occasional vascular species here are *Polygonum viviparum, Selaginella selaginoides, Empetrum atropurpureum* (at the more acid level), *Primula mistassinica, P. intercedens, Pinguicula vulgaris,* etc. Here occur:

*Lophozia quadriloba** (Fig. 55)	Arctic-Alpine
L. grandiretis (Fig. 53)	
*L. gillmani** (Fig. 62)	
L. obtusa (Fig. 56)	
*Odontoschisma macounii** (Fig. 68)	
*Scapania cuspiduligera** (Fig. 60)	
*S. gymnostomophila** (Fig. 61)	
S. degenii (Fig. 57)	
Tritomaria scitula (Fig. 69)	
*Cryptocolea imbricata**	
*Lophozia heterocolpa**	Subarctic-Subalpine
L. ventricosa	
*Tritomaria quinquedentata** (Fig. 81)	
*Blepharostoma trichophyllum**	
Scapania irrigua	

Sites Restricted to North-Facing Cliffs and Ledges Away from the Lake

All the arctic-alpine species previously listed, except for the few also occurring under present conditions, are limited to the lake shore. The few species listed below are found in the sites described largely because available moisture is high, while insolation — because of the exposure — is extremely low; furthermore, cold down-winds in the ravines may be cited as an additional factor. Finally, ice persists until late into spring in such north-facing sites lacking insolation. In both cases the arctic-alpine species are limited to "inhospitable" sites, where succession beyond the pioneer stage is virtually impossible (see Fig. 27). Hence the arctic-alpine and high subalpine species that are so often of pioneer nature have a chance to "hang on," because, essentially, of microclimatic and microedaphic conditions. Two types of sites occur here:

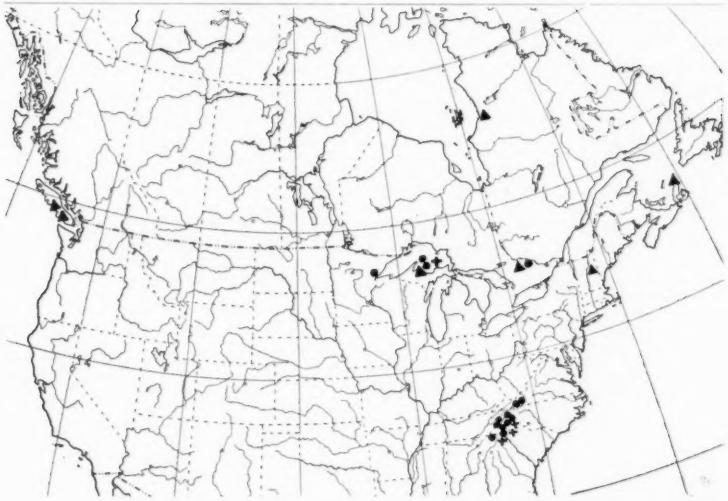


Fig. 71.—North American distribution of *Marsupella sparsifolia* (triangles); *M. paroica* (dots); *and Solenostoma appalachianum* (crosses). (Note should be taken of the fact that the Lake Superior collections of *M. sparsifolia* are of plants giving the impression of being genetically distinct. It should also be noted that the plant from Minnesota ascribed (in Part I) to *M. sparsifolia* is specifically distinct and represents *M. paroica* (Schuster 1957a); this plant has a range similar to the Appalachian-Lake Superior *Solenostoma appalachianum*.).

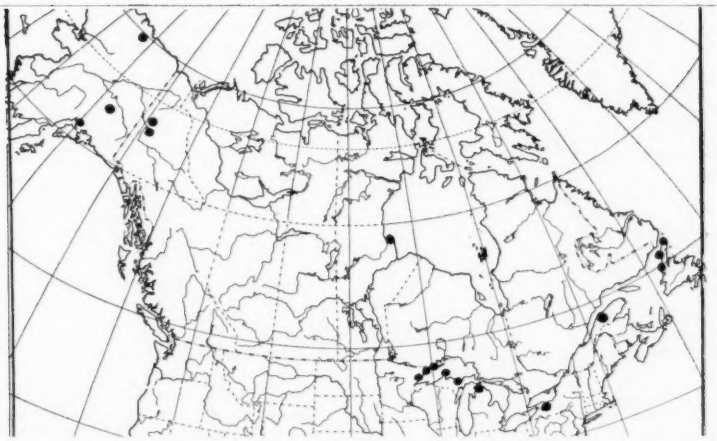


Fig. 72.—North American distribution of *Lophozia schultzii*.

A. The north-facing sides of ravines, near (1-5 feet above) the streambed, where spray and water-cooled air are important factors, and where humidity is usually nearly maximal. The Manitou, Gooseberry, Temperance, and Cascade river ravines are typical examples. Vascular species are absent, except for a few ferns and fern allies (*Equisetum variegatum;* locally *Cryptogramma stelleri* in basic sites; *Woodsia alpina* and *W. glabella*). Here occur:

Scapania degenii (Fig. 57) *S. cuspiduligera** (Fig. 60) *S. gymnostomophila** (Fig. 61) *S. buchii* (Fig. 73) *Tritomaria scitula* (Fig. 69) *Solenostoma sphaerocarpum* (Fig. 80) *S. schiffneri** *Lophozia gillmani** (Fig. 62)	Largely Arctic-Alpine in Distribution
*Lophozia badensis** *L. heterocolpa** *Preissia quadrata** *Pellia fabbroniana*	More Ubiquitous in the Subarctic-Subalpine

B. The north-facing sides (chiefly crests) of high ledges, on the south side of lakes (Gunflint Lake, Clearwater Lake) or rivers (Pigeon River) often with *Saxifraga aizoon* var. *neogaea, Lycopodium selago.* Here, on moist sites, occur a few arctic-alpine species, but many more subarctic forms:

1. On acid, igneous rocks, chiefly:

Lophozia hatcheri (Fig. 70 *Diplophyllum taxifolium* var. *macrosticta* *Scapania buchii* (Fig. 73)	Arctic-Alpine
Lophozia longidens *L. attenuata* *Tritomaria quinquedentata** (Fig. 81) *Ptilidium ciliare** *Scapania nemorosa* *Anastrophyllum michauxii*	Ubiquitous in the Subarctic-Subalpine

This type of epipetric community is very similar to the ledge and cliff wall associule occurring near the lake shore, differing only in lacking such arctic-alpine forms as *Anastrophyllum saxicolus,* etc.

2. On calcareous shales and slates (as at Mt. Rose, Grand Portage):

Asterella ludwigii (Fig. 58) *Mannia pilosa* (Fig. 59) *Scapania gymnostomophila** (Fig. 61) *Cephaloziella arctica**	Arctic-Alpine
Cephaloziella starkei *Plagiochila asplenioides**	Ubiquitous in the Subarctic-Subalpine

On such cliffs are associated such essentially arctic and alpine ferns as *Woodsia cathcartiana* (*oregana* complex), *W. scopulina, W. alpina, W. glabella,* and the more ubiquitous *Cryptogramma stelleri.*

Summary: The species of largely arctic-alpine distribution which occur in Minnesota are restricted to a few limited sites. Except for the northwest-facing shore line of the Susie Islands, such sites occur in a very scattered disjunct fashion and do not warrant consideration as actic-alpine relict areas. The restricted area of the shore line of the Susie Islands, and at Grand Marais (as well as of such similar sites as the tip of the Keweenaw Peninsula), however, presents a somewhat different picture: the vegetation there (both as regards Hepaticae and vascular plants) is to a large extent of arctic-alpine character. It consists of species absent elsewhere in the United States (*Lophozia latifolia, L. quadriloba, Cryptocolea imbricata*), of exceedingly restricted distribution (*Odontoschisma macounii, Scapania degenii, Lophozia*

Fig. 73.—North American distribution of *Scapania buchii* (= *Scapania microphylla*).

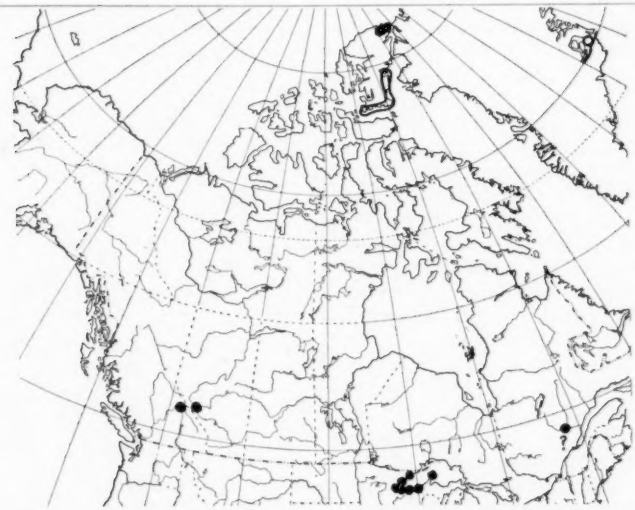


Fig. 74.—North American distribution of *Solenostoma schiffneri*. The species is ubiquitous in northeastern Ellesmere Island, and will probably prove widespread in the calcareous portions of the North American Arctic. (*S. schiffneri* is apparently conspecific with *Jungermannia polaris*, known in North America from Greenland [circle] and the southern half of Ellesmere Island [circled area]; the taxonomic problems involved are dealt with in another connection.)

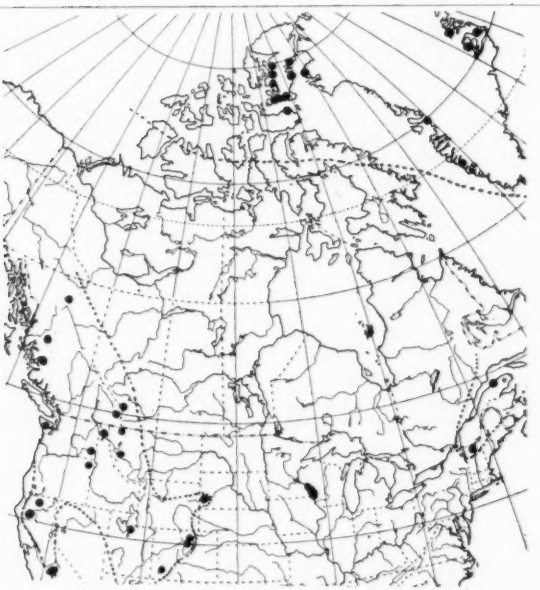


Fig. 75.—North American distribution of *Clevea hyalina*. Also very frequent in northeastern Ellesmere Island (not shown on map). The range approaches that of *Oxyria digyna*, but the latter is absent in the Midwest (see Fernald, 1933, Map 11).

grandiretis, etc.), or of subarctic species with a wide distribution in the arctic-alpine region north to at least 82° 32′ N. (*Tritomaria quinquedentata, Ptilidium ciliare, Lophozia* (*O.*) *kunzeana, Lophozia* (*Leiocolea*) *heterocolpa*, etc.). Many of these species are also cited by Böcher (1933) as occurring with the *Scirpetum caespitosi* on the Greenland coast.

Similarly, in a study of the Hepaticae of the Hudson Bay region (Schuster, 1951), I have found an essentially similar hepatic flora to occur on such tundra-covered islands as the Belcher Islands, as well as on the tundra-covered edges of the east coast of Hudson Bay (as at Cape Jones, Great Whale River, Richmond Gulf, etc.). A brief reconnaissance of the tundra at Churchill,

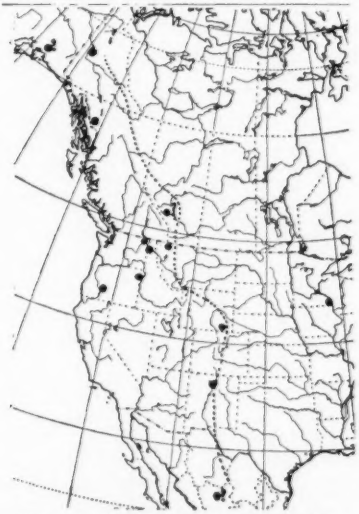


Fig. 76.—North American distribution of *Asterella saccata*.

Manitoba, revealed the presence of many of the characteristic "calciphiles" regarded as "disjuncts" in northeastern Minnesota, among them *Lophozia schultzii, L. grandiretis, Odontoschisma macounii, Scapania degenii, Cephaloziella arctica, etc.* If a list is given of the species that recur at one or more stations in the eastern sector of the Hudson Bay region (together with a few additional species reported by Lepage (1953), which appear to be from

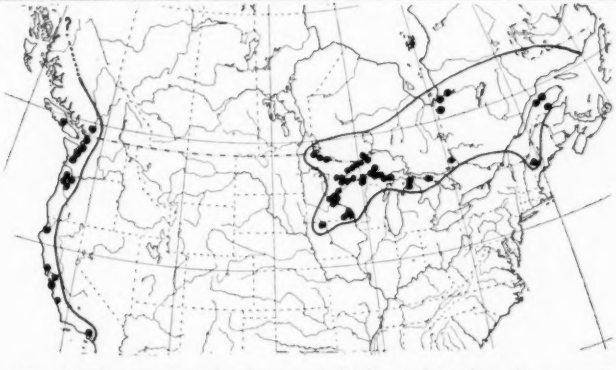


Fig. 77.—North American distribution of *Frullania bolanderi*, the two centers of extant distribution outlined; also presumably in Newfoundland. Range almost identical with that of *Streptopus amplexifolius* var. *denticulatus* + var. *oreopolus* (see Fassett, 1935, Map 2).

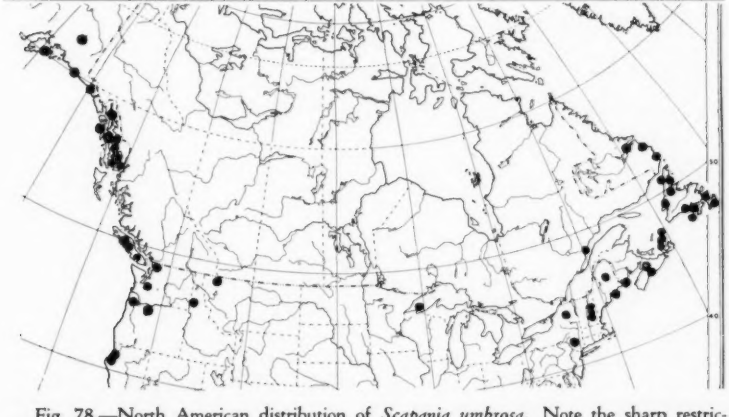


Fig. 78.—North American distribution of *Scapania umbrosa*. Note the sharp restriction to the Spruce-Fir Biome. Reports of the species from Indiana and Minnesota (in Frye and Clark), and from Greenland (in Jensen) are believed to be incorrect. Range closely similar to that of *Streptopus amplexifolius* var. *americanus* (see Fassett, 1935, Map 1), and approaches that of *Lobelia dortmanna* (see Fernald, 1933, Map 8).

the tundra edge), and compared with the arctic-alpine (and subarctic) species from the northeastern corner of Minnesota, a surprising degree of similarity in the elements present will be noted. Table I is such a list. The high degree of overlap between the list of species from northeastern Minnesota and the Hudson Bay region and the species known from northern Ellesmere Island (82° 25′-82° 32′ N.) is also to be noted. (The latter data is based on field work during the summer of 1955; this will be reported on in detail elsewhere).

Of the 91 species listed from the Hudson Bay area (including the last three species, which have been found further northward only) 67 species have been found in northeastern Minnesota in the restricted region around Lake Superior, and/or in the so-called "driftless area" of southeastern Minnesota. Another seven species occur elsewhere in the Lake Superior region. Therefore, 74 species (81 per cent) of the species known from the tundra or its periphery of the eastern portion of the Hudson Bay region are also present in the hepatic flora of the Lake Superior region.

In this connection, it may be of interest that of most of the truly arctic-alpine species only sterile material (or in the case of dioecious species, material of one sex) is known from the state. For instance, I have been able to find about 15 colonies of *Scapania degenii* var. *dubia* (the form with largely 2-celled mature gemmae) ranging over most of the Susie Islands, south to Grand Marais, and south to the Temperance River, a linear distance of about 50 miles. Of the plants observed none had developed female inflorescences; occasionally male organs had developed. Paradoxically, the extremely closely related *Scapania degenii* (the form with 1-celled gemmae) occurs in the Lake Superior region only in the female sex (Temperance R.; Belle Rose I.). All

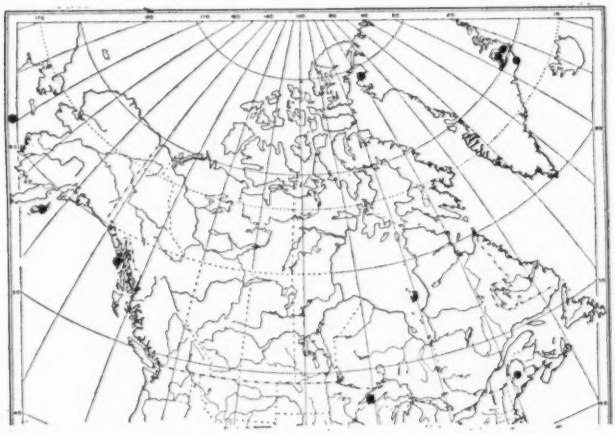


Fig. 79.—North American distribution of *Scapania scandica*. This species is not treated in Part I of this work, having been found in the Great Lakes region (Oak Island, Apostle Islands, Wis.) only recently. Also just reported from Newfoundland by Buch and Tuomikoski (1955). This species is generally oceanic in range; the report from Mt. Katahdin, Maine is a new one.

TABLE I.

	Present in N.E. Ellesmere Island (82° 25'-82° 32' N.)	Present in Hudson Bay Region (53 - 60° N.)	Present in N.E. Corner of Minnesota (47 - 48° N.)
Lophozia (O.) atlantica	(x)[1]	x	x
Lophozia (O.) quadriloba	x	x	(x)[2]
Lophozia (O.) kunzeana	x	x	x
Lophozia (O.) binsteadii	.....	x	.....
Lophozia (O.) floerkei	x	x	.....
Lophozia (B.) barbata	.....	x	x
Lophozia (B.) hatcheri	.....	x	x
Lophozia (B.) lycopodioides	(x)	x	(x)[2]
Lophozia (M.) grandiretis	.....	x	x
Lophozia (L.) heterocolpa	x	x	x
Lophozia (L.) gillmani	x	.....	x[2]
Lophozia (L.) obtusa	(x)	x	(x)
Lophozia (L.) muelleri	x	.....	x[3]
Lophozia (L.) badensis	x	x	x
Lophozia (D.) alpestris	x	x	x
Lophozia (D.) longidens	.....	x	x
Lophozia (D.) ventricosa	x	x	x
Lophozia (D.) wenzelii	x[4]	x	(x)[4]
Lophozia (D.) excisa	x	x	x
Lophozia (D.) latifolia	x	.....	x
Lophozia (I.) bicrenata	.....	x	x
Gymnocolea inflata	.....	x	x
Temnoma setiforme	(x)	x	.....
Anastrophyllum (S.) minutum	x	x	x
Anastrophyllum (E.) saxicolus	.....	x	x
Saccobasis politus	(x)	x	.....
Tritomaria scitula	.....	x	x
Tritomaria quinquedentata	x	x	x
Nardia geoscyphus	.....	x	.....
Solenostoma oblongifolium	.....	x	.....
Solenostoma obovatum	.....	x	.....
Solenostoma subellipticum	.....	x	.....
Solenostoma sphaerocarpum	(x)	x	x
Solenostoma hyalinum	.....	x	x
Gymnomitrium concinnatum	x	x	.....
Marsupella sparsifolia	.....	x	x

[1] The species, in column 1, listed within parentheses have been found in the portion of Ellesmere Island south of lat. 80° N. (largely between 76-79° lat. N.), but not yet north of there.

[2] These species are not yet known from Minnesota, but occur in either Wisconsin or Michigan, in the vicinity of Lake Superior.

[3] These species are not certainly known from the Lake Superior area, but occur to the south in the "driftless area."

[4] Represented by the very similar *L. groenlandica*, a species generally considered in the recent literature as identical with *L. wenzelii* (and so considered in Part I of this work).

[5] Not present in the area according to Schuster (1951) or Lepage (1953), but present immediately to the north of the area (Polunin, 1947).

TABLE I.—(Continued)

	Present in N. E. Ellesmere Island (82° 25'-82° 32' N.)	Present in Hudson Bay Region (53-60° N.)	Present in N. E. Corner of Minnesota (47-48° N.)
Plagiochila asplenioides	x	x	x
Mylia anomala	.....	x	x
Mylia taylori	.....	x	.....
Lophocolea minor	.....	x	x
Geocalyx graveolans	.....	x	x
Diplophyllum taxifolium	(x)	x	x
Diplophyllum apiculatum	.....	x?	x
Diplophyllum albicans	.....	x	.....
Scapania degenii	.....	x	x
Scapania hyperborea	.....	x	.....
Scapania cuspiduligera	x	x	x
Scapania irrigua	.....	x	x
Scapania gymnostomophila	x	x	x
Scapania calcicola var. *ligulifolia*	.....	x	.....
Scapania parvifolia	.....	x	.....
Scapania curta	.....	x	(x)[2]
Scapania mucronata	.....	x	x
Scapania paludicola	.....	x	x
Scapania subalpina	.....	x	x
Scapania simmonsii	(x)	x	.....
Scapania undulata	(x)	x	x
Cephaloziella byssacea	.....	x	x
Cephaloziella arctica	x	x	x
Cephaloziella elachista	.....	x	x
Cephaloziella hampeana	.....	x	x
Cephaloziella elegans	.....	x?	x
Cephaloziella rubella	.....	x	x
Cephaloziella subdentata (spinosa)	.....	x	x
Cephalozia ambigua	(x)	x	x
Cephalozia affinis	.....	x	x
Cephalozia bicuspidata	.....	x	x
Cephalozia media	.....	x	x
Cephalozia loitlesbergeri	.....	x	x
Cephalozia pleniceps	.....	x	x
Cephalozia leucantha	.....	x	x
Cephalozia lammersiana	.....	x	x
Cladopodiella fluitans	.....	x	x
Odontoschisma macounii	x	x	x
Odontoschisma elongatum	.....	x	(x)[2]
Anthelia juratzkana	x	x	(x)[2]
Anthelia julacea	.....	x	.....
Pleuroclada albescens var. *islandica*	.....	x	.....
Ptilidium ciliare	x	x	x
Blepharostoma trichophyllum	(x)	x	x
Blepharostoma trichophyllum var. *brevirete*	x	x	.....
Lepidozia reptans	.....	x	x
Calypogeia trichomanis	.....	x	x
Calypogeia muelleriana	.....	x	(x)[2]

TABLE I.—(Continued)

	Present in N. E. Ellesmere Island (82° 25'-82° 32' N.)	Present in Hudson Bay Region (53-60° N.)	Present in N. E. Corner of Minnesota (47-48° N.)
Calypogeia meylanii	.....	x	x
Calypogeia neesiana	.....	x	x
Radula complanata	.....	x	x
Pellia epiphylla	.....	x	x
Riccardia pinguis	x	x	x
Blasia pusilla	.....	x	x
Preissia quadrata	x	x	x
Marchantia polymorpha	(x)	x	x
Mannia pilosa	.....	x[5]	x
Asterella ludwigii	(x)	x[5]	x
Clevea hyalina	x	x[5]	x[3]

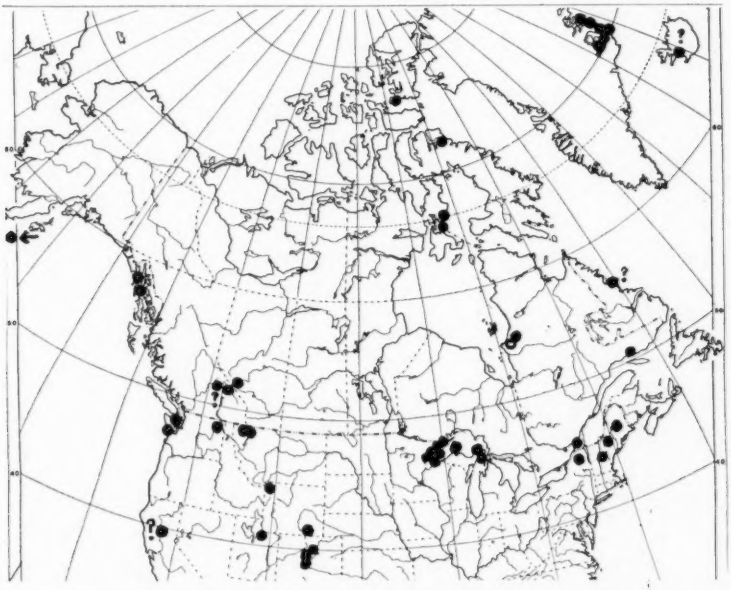


Fig. 80.—North American distribution of *Solenostoma sphaerocarpum* (dots) and the allied *S. pusillum* (rings), showing a generalized range from Arctic to Subarctic, with a cordilleran extension southward.

plants known locally of *Lophozia grandiretis* are male; all plants of *Anastrophyllum saxicolus*, female; all of the plants of *Diplophyllum taxifolium* var. *macrosticta*, male; all plants of *Tritomaria scitula*, male.

The reduction of several of the species to what appear to be single clones seems correlated with restriction in occurrence to the periphery of the hypothetical "Arrowhead Enclave."

FLORISTIC AFFINITIES OF THE DISJUNCT ELEMENTS

In this section an attempt will be made to classify the disjunct floral elements as to their floristic relationships. This will be followed by a consideration of the implications of occurrences of these types. Finally, we will examine the question of the "driftless area" as a possible refugium during the last glaciation, and the possibility of the rove slate area in the northeastern corner of the state as having served in a similar (but less widespread) manner, at least during the latter stages of the Pleistocene.

1. *Classification into Floristic Elements.*—The origin of the "disjunct" elements in the Great Lakes flora has been discussed in detail previously for the vascular plants by Fernald (1925, 1935), Fassett (1931), and for the bryophytes by Steere (1937). Both Fernald (1935) and Fassett (1931) agree in not stressing the "driftless area" as of importance as a refugium for the disjunct and especially the "cordilleran" species. Since, on the basis of study of the distribution of both bryophytes and vascular plants, I have come to an opposite conclusion, the evidence may well be discussed at some length.

Steere (1937, p. 11) identifies four disjunct elements in the bryophyte

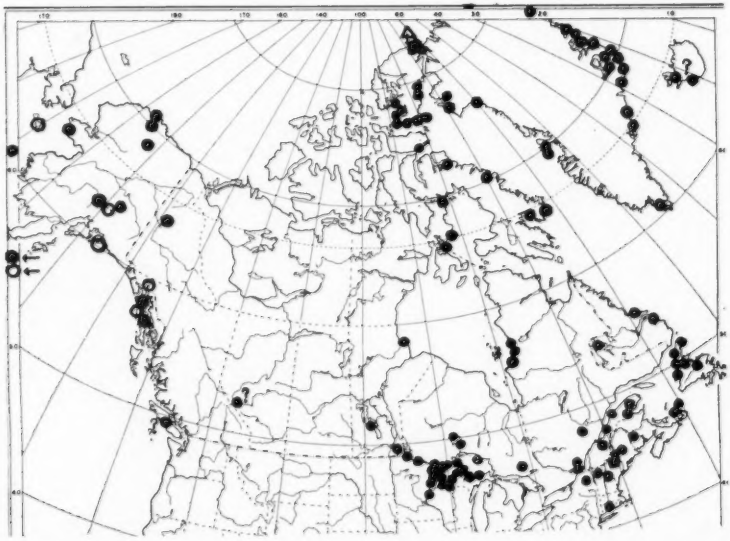


Fig. 81.—North American distribution of *Tritomaria quinquedentata;* a species of general distribution in Arctic and Subarctic regions, except in the southern Rocky Mountains and coastal ranges. Dots: typical *T. quinquedentata;* circles: var. *turgida;* triangle: var. *grandiretis.* Showing a generalized, almost ubiquitous range in the Arctic and Subarctic, but without extension southward in the Cordilleras.

flora of the Lake Superior region (and of the neighboring "driftless area") as follows: 1) Arctic species (such as *Asterella ludwigii*); 2) "almost strictly Cordilleran species, and usually characteristic of high altitudes . . ." (such as "*Jungermannia*" *schiffneri*); 3) Species of the Pacific coast "and usually characteristic of lower levels" (such as *Frullania bolanderi*); 4) "Cordilleran" elements found again only in the "driftless area," but not around the shores of Lake Superior (such as *Asterella saccata*).

Study of a larger series of species, including both bryophytes and tracheophytes, shows that still other categories must be recognized. These are: 5) Arctic-alpine species usually characteristic of high altitudes and high latitudes (or both), occurring in the "driftless area," and far to the north of the Great Lakes area, but not in the Great Lakes region (such as *Clevea hyalina* and possibly *Mannia sibirica*); 6) Arctic-alpine species occurring in the "driftless area" and again in the Great Lakes area, usually found at high latitudes or high altitudes, or both (such as *Mannia pilosa*); 7) "Cordilleran" species occurring both in the "driftless area" and in the peripheral region around Lake Superior; 8) Appalachian species occurring in the "driftless" and/or Great Lakes region (such as *Diplophyllum apiculatum*);* 9. Endemic species. These are extremely rare, and apparently limited to the vascular species. Among the latter may be mentioned *Poa scopulorum* and *Oxytropis ixodes* (Butters and Abbe, 1953). The fact that the entire Great Lakes area was glaciated during the Wisconsin Glaciation obviously makes the occurrence of endemic bryophytes virtually impossible, unless the imperfect glaciation presumed by Fernald to have occurred (in the Keweenaw Peninsula, and possibly at points on the north shore of Lake Superior) can be demonstrated.

It may not be amiss to stress that speciation in the bryophytes appears to be a much slower process, at least among the temperate and boreal forms, than among the angiosperms. Hence, the lack of development of endemic species is scarcely surprising. In the eastern half of North America it is only in the southern Appalachians where there has been the development of endemic species (*Dianthelia steerei, Plagiochila caduciloba,* etc.).

Only two species of Hepaticae have been described which initially appeared confined to the Lake Superior region, *Lophozia latifolia* and *Cryptocolea imbricata*. They are now known to occur northward to northern Ellesmere Island (Fig. 65).

The above outline of vegetational elements demonstrates that, though the majority of our species of Hepaticae, as well as vascular plants, show a "normal" predictable distribution pattern consistent with normal postglacial dispersal patterns, a number of species show peculiarities in distribution that are not clearly explicable on such a basis. These species, the "disjuncts," are phytogeographically most challenging and interesting. For that reason, the

* Fernald (1935, maps 4, 5) lists such ferns as *Asplenium cryptolepis* and *A. montanum* which have the bulk of their distribution in the ancient, unglaciated Appalachian region, with disjunct occurrences as far northwestward as the Keweenaw Peninsula. *Pellaea atropurpurea,* which occurs in the southeastern tip of Minnesota (Houston Co., near Reno) has a somewhat analogous distribution, and occurs again on the Keweenaw Peninsula. Possibly *Jeffersonia diphylla,* with a wide distribution in the Appalachians and a very limited one in southeastern Minnesota (Whitewater State Park, Beaver Valley State Park) may be classed in this category.

first seven of the categories listed above are discussed on the following pages. It is hoped that this discussion may clarify the concept that the "driftless area" occupies a special place in explaining regional plant distribution.

ARCTIC AND ALPINE SPECIES OCCURRING AROUND LAKE SUPERIOR, BUT NOT IN THE "DRIFTLESS AREA"

As has been emphasized before some members of this rather large group of species can be regarded as having a more or less continuous distribution, rather than as disjuncts.** The species of this group include:

Scapania gymnostomophila† (Fig. 62)
Scapania subalpina
Scapania degenii (Fig. 57)
Scapania buchii (Fig. 73)
Scapania cuspiduligera† (Fig. 60)
*Odontoschisma elongatum** (Fig. 65)
Odontoschisma macouniit (Fig. 68)
Lophozia grandiretis (Fig. 53)
Lophozia gillmani† (Fig. 62)
Lophozia kunzeana† (Fig. 54)
*Lophozia quadriloba*** (Fig. 55)
*Lophozia obtusa** (Fig. 56)
Lophozia atlantica
Lophozia hatcheri (Fig. 70)
*Lophozia lycopodiodes**
Lophozia schultzii (Fig. 72)
Cephaloziella subdentata (Fig. 63)
Cephaloziella arctica†
Anastrophyllum saxicolus (Fig. 67)
Diplophyllum taxifolium var. *macrosticta*
Tritomaria scitula (Fig. 69)
*Anthelia juratzkana**† (Fig. 64)
Asterella ludwigii (Fig. 58)
*Solenostoma levierii**
Solenostoma schiffneri† (Fig. 74)
Solenostoma sphaerocarpum (Fig. 80)

In addition we may mention several species occurring very commonly in the Tundra region, but which also have been reported rather frequently from the Subarctic-Subalpine regions, among them:

*Solenostoma cordifolium**
*Diplophyllum albicans**
Lophozia heterocolpa†

Fernald (1925) has listed many of the vascular species with a distribution pattern of this type, among them:

Selaginella selaginoides
Polygonum viviparum†
Sagina nodosa
Pinguicula vulgaris
Empetrum atropurpureum
Saxifraga aizoon
Empetrum nigrum

Vascular plants with the last type of distribution have been discussed by Fernald (1935, p. 206), who distinguishes a "more conservative group of species which shares Greenland with the Great Lakes region and other, usually scattered, regions of the Northern Hemisphere. In the Great Lakes Region, as in most regions, they are localized or rare species, usually seeming like pre-Wisconsin relics there. They are mostly not pioneers today, but veterans.

**In the following lists, the species marked with an asterisk have not yet been found in Minnesota but occur either in the peripheral portion of Ontario, or in Upper Michigan. At least half of these species have other restricted occurrences below the arctic-alpine region; they, however, find their greatest frequency of occurrence in the tundra. Those species marked with a dagger (†) occur north to the Arctic Sea in northern Ellesmere Island, 82° 30′ N.

This list of conservatives includes . . . *Lycopodium selago, Selaginella selaginoides* . . . *Phleum alpinum, Poa alpina, Carex scirpoides, Polygonum viviparum, Sagina nodosa, Pinguicula vulgaris.* . . ." I have previously noted that, at least in the Lake Superior region, the "more conservative species" are, in one sense at least, scarcely glacial relics, since they occur in a very narrow zone under climatic conditions that appear to be nearly optimal today, and analogous to those under which they occur, for instance, in the southern portion of the Greenland coast.

As I have been able to ascertain, both at Grand Marais, and on the Susie Islands (and nearby Pigeon Point), in Cook County, Minnesota, and on the small islands northwest of Isle Royale, Michigan, it is obvious that the so-called "conservatives" today occupy a very narrow zone and are extremely localized in occurrence. They normally occur only within 1-20 feet of the lake shore, and rarely occur more than 1-10 feet above the level of the lake. For instance, *Selaginella selaginoides* occurs at Grand Marais and on the Susie Islands, as well as around Isle Royale almost always at elevations of 1-15 feet above the lake, and never far back from the wave action zone. *Sagina nodosa* occurs at the very edge of the water on Sailboat Island, and at 2-10 feet above the lake level on Big Susie Island, Susie Islands. *Polygonum viviparum* occurs associated with the *Selaginella* at the south end of Lucille Island, on Susie Island, and at Grand Marais, as well as on the islands grouped around Isle Royale, always within a few feet of the edge of the lake. The rest of these species all exhibit largely the same distribution pattern, with the possible exception of *Lycopodium selago*. It is therefore apparent that these far northern types are restricted to a microclimatically and edaphically controlled "Tundra zone," not too dissimilar in its composition to the "Tundra zone" along the southern Greenland coast.

Böcher (1933), for instance, describes a *Scirpus cespitosus* community from the Greenland coast, which recurs on the shores of most of the Susie Islands, and on some of the small islands near Isle Royale. Associated with this, both in Greenland and in the small islands in Lake Superior are such species as *Empetrum nigrum, Selaginella selaginoides, Euphrasia* sp., *Pinguicula vulgaris, Primula* sp., as well as such Hepaticae as *Odontoschisma macounii*.

The significance of these outliers of the "Tundra zone" should be emphasized. The species that occur there are mostly members of the mesophytic or mesohygrophytic pioneer rock pool community described for Isle Royale by Cooper (1913). They would scarcely be expected to survive on the dry, windswept nunatacks that Fernald promulgates for the Great Lakes region. As will be developed elsewhere, there is no reason why at least some of these species might not have survived the Pleistocene in the "driftless area." Indeed, at least a few species belonging to this rock pool flora still survive today in the "driftless area" or at its periphery: among them *Primula mistassinica* (in Illinois, Iowa, and Wisconsin), and *Potentilla tridentata* (in Minnesota). *Lycopodium selago*, though absent from the "driftless," occurs near its periphery. These species, when occurring in the "driftless," where climatic conditions today are far from optimal, are distinct "glacial relicts"; their occurrence around the periphery of Lake Superior the writer would hardly interpret as "relict."

Most of the arctic-alpine and high subarctic species have not been found in the "driftless area," and it is doubtful if many of them can be located there. However, there is no reason why they should not have occurred there during the Wisconsin Glaciation. The occurrence in the "driftless" of species such as *Potentilla tridentata, Arctostaphylos Uva-ursi, Primula mistassinica, Mertensia paniculata, Cornus canadensis, Hylocomium splendens, Hypnum imponens, Scapania mucronata, Mannia pilosa, Tritomaria exsecta* and *exsectiformis, Woodsia cathcarthiana, Lophozia incisa,* and *Sorbus dumosa* (i.e., all species occasional to abundant in the "Tundra Strip" along the lake shore, and often associated closely with species of the above list of arctic-alpine forms) seems significant to the writer. (See discussion pp. 316-324).

"CORDILLERAN" SPECIES OF HIGH ALTITUDES OCCURRING AROUND LAKE SUPERIOR BUT NOT IN THE "DRIFTLESS AREA"

Only a very few Hepaticae in the region show a distribution of this type. Steere (1937) mentioned "*Jungermannia schiffneri* (= *Solenostoma schiffneri*) as an example (see Fig. 74). In the light of further accumulated distribution data regarding this species, we can scarcely maintain it as a "cordilleran" type, since it is known from Quebec, and I have recently found it to be common on Ellesmere Island. The distribution pattern of this species therefore emerges as essentially an arctic-alpine and high subarctic one. Steere also cites "*Jungermannia*" *sphaerocarpa* (=*Solenostoma sphaerocarpum*) as a species with a distribution of this type (Fig. 80). This, however, is also known from New England, Greenland, and has recently been reported from Quebec (see Lepage, 1945, 1953) and from the eastern Arctic region (Polunin, 1947). Indeed, the species is scarcely more restricted in occurrence than ubiquitous arctic and subarctic species as *Tritomaria quinquedentata* (Fig. 81). Some of the mosses cited by Steere (*loc. cit.*) appear to be more valid representatives in this regard. Superficially more valid examples of "cordilleran" species occurring in the Great Lakes area may be the "calciphytes" *Lophozia gillmani* (Fig. 62) and *Tritomaria scitula* (Fig. 69). Both of these species appear to have a rather wide distribution in Alberta and British Columbia (north, in the case of the *Lophozia* to Alaska and south to Oregon), then recur again, in some abundance, in the Great Lakes region, with scattered sites northeastward in the St. Lawrence Valley and in the case of *Tritomaria scitula,* in the eastern Hudson Bay area (Schuster, 1951). This distribution pattern centering about the Gaspé and St. Lawrence, western Newfoundland, the Great Lakes, and the Far West, is the classical one discussed by Fernald (1925). The writer, however, is somewhat suspicious of the disjunct nature of this distribution pattern. It reflects more a "distribution of collecting activity" and of calcareous habitats, rather than that of plant distribution. Note, for instance, the fact that until 1951 *Tritomaria scitula* could be considered a Cordilleras-Great Lakes-St. Lawrence Valley species. Yet in 1951 the writer reported the species from the Belcher Islands, an island group in Hudson Bay that was both glaciated as well as submerged until relatively recently. Certainly, the Belcher Islands cannot be considered to be a "critical"

area. It seems almost safe to predict that these two calciphile species (*T. scitula, L. gillmani*) will also be found in the strongly (and apparently uniformly) glaciated region between Churchill and British Columbia, where areas of moist calcareous rocks occur; *L. gillmani* has recently been found common in northern Ellesmere Island. The other species showing a large "break" between the Great Lakes and the Cordilleras will almost certainly also turn up in Manitoba and Saskatchewan on further collecting by a competent bryologist. The distribution pattern of the two plants possibly also reflects a distribution of "fit environments"—e.g., moist, cold, calcareous rocks.

The absence or rarity of strictly "cordilleran types" of Hepaticae in the Great Lakes area is not surprising, since there are virtually no "cordilleran" Hepaticae. Almost all of the species known from the Cordilleras are widespread types showing a broad transcontinental range, with an extended range southward in the western mountains (see Figs. 54, 58, and 70). The essentially holarctic distribution of most of these forms needs to be stressed.

In North America, *Lophozia schultzii* appears to have a decidedly disjunct distribution pattern related to the Cordilleras-Great Lakes-Gaspé type. It has been found (see Fig. 72) from northernmost Alaska (Persson) to the Yukon, and then recurs again, not infrequently, in the Lake Superior-Michigan-Huron-Ontario area, with further stations on the Gaspé coast (Lepage, 1945), and in western Newfoundland (Buch and Tuomikoski, 1955). The report of the species by Schuster (1949) from Bergen Swamp, N. Y., is quite anomalous, however, and does not fit into this distribution pattern (unless this station can be derived from a hypothetical refugium in the unglaciated area some 100 miles to its south). The other stations all lie in or relatively near unglaciated areas. However, in the spring of 1955 the writer collected the species at Churchill, Manitoba, in an area far from any known "refugium" (compare Figs. 21 [Part II] and 72).

Fernald (1935) discusses a rather large number of vascular plants with a distribution of this type, among them the classical *Cryptogramma crispa* var. *acrostichoides* (see map 12, p. 245 in Fernald, *loc. cit.*), and *Adenocaulon bicolor* (see map 9, p. 213). A particularly interesting example is the salmon berry, *Rubus parviflorus* (see map 14, p. 272). These species, as has been stressed by Fassett (1929), show a distribution pattern that seems quite unrelated to the "driftless area." These, and perhaps some other species, as suggested by Butters and Abbe (1953) and by Stebbins (1935), may be postglacial migrants into the region via migratory routes along the borders of the retreating icefields. However, such an explanation is difficult to accept for shrubby plants such as *Rubus parviflorus* or *Oplopanax horridus;* neither is a periglacial pioneer!

SPECIES OF THE PACIFIC COAST USUALLY CHARACTERISTIC OF LOWER ELEVATIONS, ALSO OCCURRING IN THE GREAT LAKES AREA

Among the Hepaticae a single species stands out: *Frullania bolanderi* (Fig. 77). Steere (1937) cited this and included a map of its distribution, but was unable to suggest any logical reason for the unique distribution of the species. Since recent work has broadly extended the range of this species, it

now seems possible to clarify its apparently anomalous distribution. The distribution as known of this species decidedly links the "driftless area" with the Great Lakes area. *F. bolanderi* was described from San Francisco, California, and is known along the Pacific Coast, chiefly at lower levels and in temperate regions, from Vancouver Island to the southern half of California. The species appears again in north central Iowa (Emmet County), and I have records of it from the greater part of Minnesota (see Part I). It had previously been known from the eastern edge of the state, along the Lake Superior shore. It occurs again, limited largely to the lake shore, in Wisconsin (Douglas Co., at Nebagamon Falls), and in many places in Michigan (Houghton, Keweenaw, Alger, Marquette, Ontonagon, Gogebic, Barraga, Mackinac, Emmet and Cheboygan counties). Northward it occurs again in Ontario (Lake Timagami, Cain and Fulford, 1948; north of Pigeon River; commonly on Manitoulin Island, Lake Huron, and then is found again in Maine (Canton and Oxford counties), and in several stations in Quebec (see Fig. 77). Possibly also in Newfoundland (see Buch and Tuomikoski, 1955).

It is obvious from the distribution of the species that we are not dealing with an arctic-alpine element. The species is abundant in the deciduous forest regions of Minnesota, occurring even in disturbed places like Minnehaha Falls in Minneapolis, and is common in floodplain forests, on bark of elm (as at Nine-Mile Creek, Hennepin Co.), and along the deciduous forests of the bluffs along the Mississippi River, south almost to Iowa (in Winona, Fillmore and Houston counties).

The distribution of this species is highly important to an understanding of the phytogeographical affinities of the Lake Superior area. When the species was first found in the Great Lakes region, it was considered to be an outstanding rarity (see Steere, 1937, 1938), and is still considered in recent literature to be limited to the immediate vicinity of the Great Lakes (except for the single report from Emmet Co., Iowa). While known only from the immediate vicinity of the lake shore, the species gave the impression of a "cordilleran" or western type occurring as a disjunct that must have survived on a hypothetical "nunatak" area — such as that on the Keweenaw Peninsula. Such an explanation is not at all satisfactory, for several reasons: 1) The species is limited to lower elevations and is not a "cordilleran" element. As such, its survival in a "nunatak" area seems a virtual impossibility, considering the extraordinarily rigorous conditions presumed to have existed in such areas. 2) The species is almost always epidendric; we would therefore need a "nunatak" area with a well-developed forest thereon, to explain the survival of *F. bolanderi* in the immediate vicinity of Lake Superior.

With the discovery of the fact that this species ranges throughout much of the deciduous forest region, into the "driftless area," another hypothesis suggests itself: *the species survived the Wisconsin Glaciation in the "driftless area."* The latter is well-known to have had forest cover throughout the later stages of the Pleistocene, hence offered sites that would support the species. From the "driftless" there appears to have been a gradual migration of the species outward, now covering much of the Great Lakes region.

The few isolated stations for the species eastward (see Fig. 77) possibly cannot be explained on this basis. They could conceivably represent northward

migration from the unglaciated Appalachian Plateau of Pennsylvania and southwestern New York. The species should be searched for in this area.

Cephalozia leucantha may be a similar case. This is a subarctic-subalpine species, rarely occurring into the lower edge of the tundra (and first reported from there by Schuster, 1951); see Fig. 49. This species was known only from the coastal regions of western North America (Washington, Vancouver Island, coastal southern Alaska), and from the St. Lawrence region (Quebec, from the adjacent Anticosti Island, Cape Breton Island, and Newfoundland); until discovered by the writer in northeastern Minnesota, as well as in collections studied from the Hudson Bay area, and from Mt. Marcy, New York. No evidence exists, however, that this species may have survived the last glacial period in the "driftless area." Another case, needing further confirmation is that of *Cephalozia affinis*, known from the West Coast, and reported, by the writer, on the basis of one collection from the Lake Superior area. Both of these species of *Cephalozia* are, in the West Coast region, restricted to the coastal ranges or to the lowlands, and are not strictly montane species. In both cases, more extensive collections may well prove them to be boreal-transcontinental in distribution.

Among the vascular species there are relatively few with a distribution pattern of this type. The best known exception is *Oplopanax horridus*, known from the West Coast and again from Isle Royale, and the Ontario shore in the same general area. The distribution of *O. horridus*, though somewhat analogous, probably cannot as easily be explained by the same means: the species is quite absent now from any area near the "driftless." It is more probable that its present Lake Superior stations are derived from postglacial migration northward from the "driftless area," than that the species migrated "along the retreating ice fronts" from Montana eastward! Certainly, this shrubby plant is no more of a periglacial pioneer than is *Frullania bolanderi*.

"CORDILLERAN" ELEMENTS IN THE "DRIFTLESS AREA," ABSENT FROM THE GREAT LAKES REGION

Among the Hepaticae *Asterella saccata* is the most striking example (see Fig. 76). A second possible example is *Mannia sibirica*, previously known only from single stations in Norway and Siberia, and one recent station in Alaska, as well as several from southeastern Minnesota (Fig. 59), and northeastern Iowa. The distinctness of this latter species from the more ubiquitous arctic-alpine *Mannia pilosa* still needs further proof, however. The writer, therefore, would not for the present stress this as a "cordilleran" species in North America. Holzinger has reported two mosses with an apparently "cordilleran" distribution: *Grimmia raui* (from Winona, in the "driftless"; again in Colorado at about 5000 feet), and *G. wrightii*, a southwestern species, (from Winona; again from Colorado to Kansas, Texas, New Mexico). (*Didymodon rigidulus* and *Ditrichum flexicaule* also have a largely "cordilleran" range, although with stations in the east, the latter extending northward to the Arctic Ocean coast of Ellesmere Island (Schuster; unpublished).

Among the vascular plants the best known example is that of *Montia chamissoi* (= *Claytonia chamissoi*), known regionally only from Queens (Gwynn's) Bluff, 18 miles S. of Winona, but widespread in the Cordilleras.

The most striking fact about these disjuncts occurring in or within the periphery of the "driftless area" is that they have not been able to migrate from it to any degree during postglacial times. Other species, apparently localized there during the glacial period, have spread widely since: among them *Mannia rupestris, M. pilosa, Scapania mucronata, Frullania bolanderi,* etc. The reason for the continuing postglacial localization to such a limited region eastward is not clear, but possibly is due to reduction of the population to a few genotypes (due to a rigid elimination during glacial, or possibly also during postglacial times), with the consequence that these species today are "rigid" or "senescent." A similar explanation has been suggested by Scoggan (1950) to explain the highly restricted ranges of certain rare arctic and alpin species. He states that: "some of the rare species may consist of only one or a few ecotypes, unable to survive except under the peculiar conditions to which they are adapted. The hardships to which they were subjected while being forced southward by the Wisconsin ice-sheet may have substantially depleted the biotype stock. . . ." A corollary to this phenomenon would be a reduction in their ability to compete, and, of course, in their ability to expand their range.

Since Rosendahl and others have shown that the regional flora of the last interglacial period was similar to the present flora, it is difficult to explain these "cordilleran" elements in the "driftless area" as relicts of a greater preglacial distribution. The occurrence of these species there, and *nowhere else in the entire general region* also suggests that the hypothesis of migration in from the west along a fluctuating glacial boundary during late glacial times is hardly valid in explaining their anomalous distribution. In this connection, attention should perhaps be called to the moss, *Camptothecium woldenii* Grout, described from the Aftonian interglacial deposits of Iowa, of nearly one million years ago. Grout considers his species, known from the sole station in Iowa and evidently now extinct, as related most closely to *C. pinnatifidum,* a species not at present found east of the Rocky Mountains.

ARCTIC-ALPINE SPECIES OCCURRING IN THE "DRIFTLESS AREA" (AND ITS PERIPHERY) BUT NOT IN THE GREAT LAKES REGION

This group of species shows a very suggestive distribution pattern. The group is similar to the previous one ("cordilleran" species, limited eastward to the "driftless area"), differing in that the species involved show at least a few localities also in the arctic-alpine region to the eastward, usually recurring on the coast of Greenland. Indeed, there is hardly a sharp distinction between the two groups.

Among the Hepaticae, there are only two species showing this distribution pattern in a classical sense: *Clevea hyalina* (Fig. 75), found in S. E. Minnesota in eight different sites by the writer (1947-1950), and *Mannia sibirica* (Fig. 59) found in S. E. Minnesota and N. E. Iowa in 11 different sites by the writer (1947-1950). The latter species, reported from a single site in Alaska (Frye and Clark, 1937-1947) may be found to have an arctic-alpine transcontinental (and circumpolar) distribution; it is known elsewhere only from Norway and Siberia.

Among the vascular plants, at least three species show a similar distributional pattern: *Rhododendron lapponicum*, growing with other arctic-alpine species (such as *Primula mistassinica*, which, however, also occurs in the Great Lakes area, hence belongs to the next group in our classification) in the Dells of the Wisconsin River, but nowhere else in the entire Great Lakes region; *Sedum roseum*, isolated at a single station in Olmstead Co., Minnesota (see Rosendahl and Moore, 1947), occurring again as a rare relict in central New York and along the Delaware River, and on Roan Mt., N. C.-Tenn. border, but then recurring only very rarely until the Greenland coast is reached. A third species, *Chrysosplenium iowense* Rydberg, is of particular interest in that the type of this largely arctic-alpine plant came from the periphery of the "driftless area" in Iowa, while the main body of its distribution appears to be far north of there. Rosendahl (1947) reports it not only from Iowa (Winneshiek, Dubuque, Fayette, Allamakee counties in N. E. Iowa), but from Alberta (forest edge 100 miles N. of Edmonton; Elbow R. in the Rocky Mountains; 12 miles N. of Edmonton; Ft. Saskatchewan; Slave Lake district), and from District of Franklin (Victoria Island; Baffin Island). Rosendahl (*loc. cit.* p. 34) states: "The isolated occurrence of the species in northeastern Iowa presents a striking case of disjunct distribution and another instance of a Pleistocene relict holding out in or on the edges of the "driftless area." It is mostly limited to cold-water seepage places on north-facing wooded bluffs . . .; it grows at the entrance to an ice-cave and in Pine Hollow, Dubuque County, at the entrance to a cool cave." The writer would also like to stress the very small size of *Chrysosplenium* — so small that it can be said to be dependent on microenvironments for its survival, exactly like *Clevea* and *Mannia*.

ARCTIC-ALPINE (AND SUBARCTIC-SUBALPINE) SPECIES OCCURRING IN THE "DRIFTLESS AREA" AND AROUND THE PERIPHERY OF LAKE SUPERIOR

This group of species (whose sum-total distribution is equal to that of the first group, and the immediately preceding group combined) is phytogeographically most important since it indicates a fundamental similarity of these two groups. Furthermore, the fact that a fairly large number of species of vascular plants are found both in the "driftless area" and along the north shore of Lake Superior adds to the evidence that the "driftless area" may have served as a refugium during the Wisconsin glaciation for some of the present-day flora existing around the Great Lakes area.

Among Hepaticae *Mannia pilosa* (Fig. 59) is the best example. This arctic-alpine species occurs amphizonally in Minnesota and Wisconsin: in and near the "driftless area," and somewhat to the north (as at Osceola, Wis.; Lake City, Minn.), in the deciduous region, and then again in the coldest portions of the upper corner of Cook and Lake counties, together with other essentially arctic-alpine species (*Asterella ludwigii, Cephaloziella arctica, Scapania gymnostomophila*). The species, elsewhere in North America, is almost strictly arctic-alpine in distribution, scarcely penetrating into the Coniferous-Subarctic zone.

Other species more strictly subarctic in distribution (but common around

the periphery of Lake Superior) that occur in the "driftless area" are such Hepaticae as *Tritomaria exsecta* and *exsectiformis* (see Conklin, 1929; Conard, 1945), *Lophozia incisa* (see Conklin, 1929), *Scapania mucronata* (found by the writer at Winona and at Gwynn's (Queen's Bluff), *Ptilidium ciliare;* and such vascular plants as *Primula mistassinica, Potentilla tridentata, Equisetum scirpoides,* etc. Among other subarctic species isolated there are *Arctostaphylos Uva-ursi* var. *coactilis, Thuja occidentalis, Abies balsamea, Cornus canadensis, Moneses uniflora, Pyrus dumosa, Pinus banksiana, Acer spicatum,* etc. The occurrence of these species *both* in the "driftless area" and in the region fringing Lake Superior is commented upon in greater detail in the following section.

"CORDILLERAN" SPECIES OCCURRING BOTH IN THE "DRIFTLESS AREA" AND IN THE PERIPHERAL REGION AROUND LAKE SUPERIOR

No bryophyte species known to me has this distribution, and apparently very few species of vascular plants have such a distribution. However, *Mertensia paniculata,* an essentially subarctic to low arctic species, common in the area around Lake Superior, and occurring again scattered throughout the Cordilleras (often at high altitudes), but occurring no further eastward, has recently been found in the "driftless area" of Minnesota (balsam grove west of Wykoff, Fillmore Co.), as well as from Iowa (near Decorah; see Williams, 1937). Possibly also belonging in this group is *Carex praegracilis* W. Boott (= *C. marcida* Boott). This species has been reported by Fernald, 1935, pp. 252-253) from Eagle Harbor, Keweenaw Co., Michigan, and by Fernald (1950) from Iowa.

It may be more than coincidental that, except for its occurrence in and near the "driftless area," *Mertensia paniculata* has a distribution pattern very similar to that of *Rubus parviflorus.*

Summary.—An analysis of the preceding seven distributional types suggests that the more or less disjunct ranges of the species which have been discussed cannot be uniformly explained by the several hypotheses which have been given (Fernald, 1935; Butters and Abbe, 1953) in recent years to account for the distribution of the disjuncts of the Upper Midwest. The disjunct elements in some cases (e.g., that of *Frullania bolanderi*) cannot have readily survived on barren, treeless nunataks, nor can they be considered periglacial pioneers. Current theory, especially that in Butters and Abbe (1953), does not suffice to explain all existing distributional anomalies. Such theories, in which the significance of the "driftless area" is denied either implicitly or explicitly, also fail to explain the occurrence in the "driftless area" of a series of arctic, or arctic-alpine and "cordilleran" species, both of herbaceous angiosperms and of bryophytes, some of which also occur as isolated populations in the Lake Superior region. The occurrence today in the "driftless area" of species such as *Clevea hyalina* and *Chrysosplenium iowense,* to cite only two examples, points sharply to this region as a Pleistocene refugium for a variety of species of arctic and/or "cordilleran" species, of which the majority are postulated to have died out in that area during or perhaps even before the period of the "climatic optimum." The "driftless area" thus must be con-

sidered as at least a possible supplementary source for revegetation of the Lake Superior region during the postglacial times. This thesis was originally outlined by Fernald (1925), and is re-evaluated in some detail in the concluding section of the present work.

One of the most interesting facts to emerge from study of a long series of species of Hepaticae of northern distribution is that there is no sharp distinction between arctic species and "cordilleran" species. Indeed, it is shown that no "cordilleran" Hepaticae are to be found in the Lake Superior region, while only *Asterella saccata*, occurring in the "driftless area," may be considered as having "cordilleran" distribution. In fact, the total lack of any sharp distinction between arctic-alpine and "cordilleran" types of distribution is clear when the distribution maps (Figs. 54-74, 80-81) are compared. Fassett (1941, p. 341, maps 29-34) also gives a number of maps of "Cordilleran" and "Boreal" species, showing gradual intergradation from a typical "cordilleran" range, with isolated stations in the Great Lakes (*Rubus parviflorus*, for example), to boreal types (such as *Populus balsamifera*). Fassett concluded that discontinuities, or gaps, in postglacial distribution are due in part to "varying tolerance to low humidity in the region between the Great Lakes and the moist ravines of the western mountains."

The fallacy of considering such species of Hepaticae as *Solenostoma sphaerocarpum* as "cordilleran" in range is clear when the known range of this species (Fig. 80) is compared with that of a widespread arctic and subarctic species such as *Tritomaria quinquedentata* (Fig. 81). The differences in sum-total distribution of these two species fail to show any phytogeographical significance, and rather reflect two factors: (a) A greater rarity of the *Solenostoma* as compared to the *Tritomaria;* (b) The small size and less conspicuous appearance of the *Solenostoma.* As a consequence, the writer would propose to drop the term "cordilleran" as describing the distribution of the few Hepaticae (*Solenostoma schiffneri, S. sphaerocarpum*) for which it has been suggested. It is probable that an explanation of the phenomenon of a "cordilleran" vs. an "arctic-alpine" range is to be found in the following well-known facts: (a) Glaciation was far less extensive in the West than in the East, large areas of Alaska and most of the western United States having been free of all but local montane glaciation during the Pleistocene. In contrast, in the East only the southern portions of the old Appalachian upland escaped *both* glaciation and marine action in the period since the Cretaceous (see Fig. 21); (b) As a consequence, survival of many species in the West, both in the western Yukon and Alaska, and in the Rocky Mountain region and elsewhere, was possible during the Pleistocene, while there was extensive extinction of these species in much of eastern North America. (c) The species which underwent extinction (wholly or in part) in the East differed in their ability to reinvade the eastern portion of their former ranges, leading to (d) A considerable range of differences in the *extent* to which these species have been able to re-establish themselves in the East. (Compare Figs. 54-74, 80-81.) As has been suggested, the strategic position of the "driftless area," together with the fact that such "cordilleran" species as *Asterella saccata* and *Mertensia paniculata* still occur there today, suggests that it may have served as a partial refugium for some of the elements that have been able to re-

invade, to a greater or lesser extent, the old "eastern portions" of their former ranges. The strategic importance of a species such as *Frullania bolanderi*, which is of wholly non-arctic affinity, in any such explanation is obvious from the preceding discussion.

A possible, even if minor, source of revegetation of the northern species may have been the various non-glaciated or locally glaciated regions lying in the far north (as from the locally glaciated Greenland coastline; from the presumably only locally glaciated northernmost edge of the Canadian Arctic archipelago, etc.). Revegetation from these regions, however, cannot have served as a source for the populations in the Great Lakes region. Equally possible as a source of revegetation for the subarctic (and in some cases the oceanic or suboceanic) species may have been the northern end of the Appalachian Plateau. A study of Fig. 78 (*Scapania umbrosa*) and Fig. 79 (*Scapania scandica*) lends some support to such hypotheses. In both instances we deal with species of some frequency in oceanic and suboceanic regions. Both species, furthermore, occur as great rarities and as isolated populations in the Lake Superior area. It could be postulated, in the case of *Scapania scandica* that the species survived the Pleistocene in the Northwest in the unglaciated portions of Alaska, while in the East it survived presumably on the locally ice-free nunataks along the Greenland coast, and possibly in similar situations elsewhere. *S. scandica* has been found only recently in continental North America. Persson (1952) reported it from several stations in Alaska, and Buch and Tuomikoski (1955) from Newfoundland. I had previously found it (1949, 1954) on Mt. Katahdin, Maine, and in 1954 found a collection of the species from Oak Island in the Apostle Isls., Wisconsin, in the herbarium of the New York Botanical Garden. The latter was originally believed to be closer to *S. helvetica*, a very closely allied species certainly known only from central Europe, but the late Dr. K. Müller in 1954 examined it and pronounced it closer to *S. scandica*. The species has been considered to be sharply oceanic in range, a distribution which is clear from Fig. 79, if the wholly isolated station from Lake Superior is omitted.

The less "northern" *Scapania umbrosa*, in contrast, could have survived westward in the Cordilleras and eastward in the Appalachians. (It occurs today south to Slide Mt., New York, very close to unglaciated areas.) However we attempt to explain the eastern and western ranges of these two species, the wholly disjunct occurrence in the Apostle Island region of Wisconsin remains almost inexplicable (the Apostle Islands having been wholly submersed in immediate postglacial times), *unless* reinvasion of these two species, limited to cool, moist areas, from a cool, moist Pleistocene refugium in the "driftless area" is assumed. Their absence today from this latter area is wholly irrelevant to such a hypothesis.

As a consequence, the "Driftless" assumes, for a variety of causes, a central position, and therefore deserves special discussion.

THE "DRIFTLESS AREA" AS A REFUGIUM

Fernald (1925, p. 317) speaks of the "driftless area" as follows: "There is . . . 110 miles south of Lake Superior . . . one of the most famous unglaciated regions within the general area of North America which was

invaded by the Keewatin and Wisconsin ice. . . . Alden points out that to the north, west and south of the 'driftless area' much of the region was invaded by glaciers only long before the Wisconsin Glaciation. This 'driftless area' and the eastern margin of the region of pre-Wisconsin drift . . . is now, of course, too hot and dry for the plants which occupy the headlands and peninsulas of Lake Superior. . . ." Though, as a generalization this is quite true for the vascular plants, which have an infinitely narrower amplitude of ecological adaptability, this is not true for many of the bryophytes, which have a remarkable amphizonal distribution. The somatic adaptability of many of the bryophytes is so great that even typically arctic-alpine species still occur today in the "driftless area" (*Clevea hyalina, Mannia sibirica*), while only a very few vascular species that are common around Lake Superior occur there (*Vaccinium cespitosum, Mertensia paniculata, Potentilla tridentata, Primula mistassinica*, etc.), and these, in general, are widespread subarctic and "low" arctic types.

Fernald goes on to state: "In view of the fact that this well-known area which was not invaded by Wisconsin ice is a definite center for plants of limited range, which there apparently outlived the Wisconsin Glaciation, it seems reasonable to suppose that the western plants which are not isolated about the Great Lakes (and particularly about Lake Superior and the northern half of Lake Michigan) found refuge during the maximum of Wisconsin glacial conditions in the Driftless or undisturbed area south of Lake Superior and, upon the melting of the ice, the general increase of temperature and the uncovering of the headlands of northern Michigan, withdrew to these hospitable areas. Such an explanation finds support, also, in the fact that the western plants which are isolated about the Great Lakes and again about the Gulf of St. Lawrence have shown in the latter region a positive ability to spread away from the unglaciated spots to adjacent glaciated areas. . . ."

Fernald's hypothesis was not underlain by much concrete evidence at that time. He did not — or could not — indicate any "cordilleran" species that occur *today* in and around the "driftless area," as well as around the Great Lakes area. So far as I am aware, in 1925 we did not know of any specific cases. (This is also clearly emphasized as late as 1937 by Steere (1937a) who states: "The mosses and hepatics of the best known driftless area are so inadequately known that only a few examples of preglacial relict species can be identified." Of these species, Steere suggests only a single one, *Asterella saccata*.) Possibly for this reason, Fernald (1935) appears to have dropped this earlier hypothesis in favor of a hypothetical "nunatak area" near the tip of Keewenaw Point in Michigan. Similarly, Fassett (1931) has also cast doubt upon the "driftless area" as a possible refugium for a part of our boreal flora, during the last glaciation, although he had earlier (1929) expressed at least partial agreement with this thesis.

Fassett (1931) implies that since certain specific species (such as *Rubus parviflorus*) occurring around the Lake Superior margin do not occur in the "driftless area," the latter cannot have served as a refugium for the plants of the Great Lakes region. It is wholly invalid to presume that because *specific* species no longer exist in the "driftless" today, that they might not have occurred there during the Wisconsin Glaciation. The critical point, in

my mind, is the fact that some species did survive the last glaciation there and still occur there today as isolated populations. Postglacial climatic variation and fluctuation certainly must have been of critical importance in wiping out many of the glacial relics and in generally shaping the nature of the flora that today occurs in the "driftless." It is of interest to note that among the Hepaticae it is largely among the less delicate, essentially xeromorphic Marchantiales that we have had survival of arctic-alpine elements in the "driftless." Such far northern and essentially alpine, "cordilleran" or arctic-subarctic species as *Clevea hyalina, Mannia pilosa, M. sibirica, Asterella saccata,* and *Preissia quadrata* still occur today in the "driftless area." They represent, in fact, half of the Marchantiales known from the area (the ubiquitous *Conocephalum conicum* and *Marchantia polymorpha,* as well as the southern *Mannia fragrans, M. rupestris* and *Reboulia hemisphaerica,* complete the list of Marchantiinae known from the region). In contrast, none of the twenty-odd species of relatively delicate Jungermanniales that can be classed as arctic-alpine, and that occur in northern Minnesota, occur today in the "driftless area." It would seem quite possible, therefore, that many of the mesic, basiphilous northern species, such as *Pinguicula vulgaris, Selaginella selaginoides,* etc., may have at one time occurred in the "driftless area," but disappeared from there (perhaps during the "climatic optimum"), as presumably did those leafy Hepaticae (Jungermanniales) of arctic-alpine affinity that may have survived the glacial period there.

Since the suggestion by Fernald (1935) that the Keweenaw Peninsula served as a "nunatak area" has met with little or no acceptance,* it may be of interest to study the earlier suggestion by Fernald (1925, p. 317) that the "driftless area" to the southwest of the Keweenaw Peninsula may have served as a refugium.

Some evidence has accumulated that this may have been the case for vascular species: the existence today in the "driftless area" of such far northern species as *Chrysosplenium iowense, Rhododendron lapponicum, Sedum roseum, Claytonia chamissoi,* as well as the northern Hepaticae *Asterella saccata* and *Mannia pilosa* all point to the unglaciated region as a possible "refugium." No attempt had been made previously to assemble the entire accumulated evidence in favor of such a hypothesis. It is also of some significance that much of this evidence has accumulated recently. The writer's own records (*Mannia sibirica, Clevea hyalina, Frullania bolanderi, Scapania mucronata,* etc.) have all been made during the last decade. It therefore seems profitable to give a compilation of the more striking boreal and arctic-alpine (and "cordilleran") cryptogamic and vascular species present there today.

BRYOPHYTES**

1. *Asterella saccata.*—Found by Holzinger at Winona, Winona County (Fig. 76).

2. *Mannia pilosa.*—Reported first by Conklin (1942) on the basis of a specimen collected by Holzinger at Winona, and by Conard (1940, 1945)

* Objections to it, on various grounds, are raised by Bergquist (1937), Wynne-Edwards (1937, 1939), and Butters and Abbe (1953). See also the excellent review by Scoggan (1950) of the whole problem of "refugia" in eastern North America.

**For the general range of the mosses cited, see Grout (1928-1940).

from Iowa (Winneshiek Co.) and Conklin (1929) from two stations in Grant Co., Wisconsin (in the "true" unglaciated); as well as north of the "driftless," in Polk County (Fig. 59).

3. *Mannia sibirica.*—Found by the writer in scattered localities in N. E. Iowa and north to Winona, Houston, Lake counties, north to Washington Co., Minn. (Fig. 59).

4. *Clevea hyalina.*—Found by the writer in Houston, Lake and Wabasha counties, south to N. E. Iowa (Fig. 75).

5. *Scapania mucronata.*—Found by the writer in Houston and Winona counties.

6. *Tritomaria exsecta.*—Found by Holzinger at Lamoille, Winona Co., reported by Conklin (1942); also reported by Conklin (1929) from the so-called unglaciated region in Wisconsin.

7. *Tritomaria exsectiformis.*—This essentially subarctic species is reported by Conard (1945) from the so-called unglaciated region of Iowa, and by Conklin (1929) from the "driftless" of Wisconsin.

8. *Gyroweisia tenuis.*—Reported by Conard (1945) from Iowa; for the range of this species see Steere (1939); otherwise known from Owen Sound, Ontario; Houghton Co., Michigan; and Lake Manitoba, Manitoba.

9-26.—*Brotherella recurvans, Didymodon rigidulus, Distichium capillaceum Drepanocladus uncinatus, Hygrohypnum ochraceum, Hylocomium splendens, Hypnum crista-castrensis, Neckera pennata, Oncophorus wahlenbergii, Orthotrichum anomalum, Polytrichum piliferum, Rhytidium rugosum, Saelinia glaucescens, Seligera pusilla, Tortella fragilis, Trichostomum cylindricum, Grimmia raui.* These 17 species have been reported by Conard (1945) from stations peripheral to the unglaciated "driftless area," in northern and northeastern Iowa. Several of them have also been found in a balsam grove at Wykoff, Fillmore Co., in southeastern Minnesota, and the last species listed was reported by Holzinger from Winona, southeastern Minnesota. This last species (*Grimmia raui*) is more or less "cordilleran" in range, occurring again in Colorado at above 5000 feet. The other species are largely boreal, except *Didymodon rigidulus,* which is largely "cordilleran" (British Columbia, south to California, New Mexico and eastward to Texas), but recurs at Owen Sound, Ontario and in Newfoundland.

27. *Grimmia wrightii.*—A "cordilleran" and southwestern species, reported from Winona by Holzinger and again from the southwest (Colorado to Kansas, Texas, and New Mexico).

28. *Ditrichum flexicaule.* Reported by Holzinger from Winona, recurring again westward (British Columbia and Alberta) although hardly "cordilleran" in range, with several stations eastward (in Greenland, Nova Scotia, and Ontario). For the ranges of this species (and species 26 and 27) see Holzinger (1905 and 1905a). *D. flexicaule* occurs northward to N.E. Ellesmere Island and is probably general in the American Arctic.

VASCULAR SPECIES*

1. *Rhododendron lapponicum.*—See Fassett (1929); at Dells of Wisconsin R.

* For the general distribution of the vascular plants cited see Fernald (1950). The nomenclature is as in that work, therefore authorities are not cited.

2. *Chimaphila umbellata* var. *cisatlantica*.—See Fassett (1929).

3. *Moneses uniflora*.—See Fassett (1929); a single station in Grant Co., Wis., isolated far from the other stations near Lake Superior.

4. *Pyrola secunda*.—See Fassett (1929); also in Houston Co., Minn.

5. *Pyrola asarifolia*.—See Fassett (1929).

6. *Ledum groenlandicum*.—See Fassett (1929); a single station at Dells of the Wisconsin R., near *Rhododendron lapponicum*.

7. *Chamaedaphne calyculata*.—See Fassett (1929).

8. *Vaccinium cespitosum*.—Fassett (1929) states "This is one of the species accredited with preglacial age by Fernald (1925). Of the three known stations in Wisconsin, two are in the unglaciated area and one is to the north of it. This is in line with the ranges of a number of plants which seem to have survived the glacial period in this region, and to have worked northward since the recession of the ice, as, for example, *Epipactis decipiens* on the south shore of Lake Superior, and *Oplopanax horridus* on Isle Royale."

9. *Mertensia paniculata*.—Found by Rosendahl and Moore near Wykoff, Fillmore Co., Minn. in a balsam grove, and at Decorah, Iowa; otherwise this "cordilleran" species is known only around Lake Superior and westward (see Williams, 1937).

10. *Chrysosplenium iowense*.—See Rosendahl (1947). This species occurs in the "unglaciated" area of northeastern Iowa, in the Cordilleras, and north in Victoria and Baffin Land.

11. *Sedum roseum*.—This species occurs in Olmstead Co., Minnesota (see Rosendahl and Moore, 1947); it does not recur again until the Labrador-Greenland coasts are reached, excepting a few relict stations in New York, and one on Roan Mt., N. C.-Tenn. (The distribution of this species closely parallels that of *Rhododendron lapponicum*, but the latter does not extend south in the Appalachians).

12. *Claytonia chamissoi*.—This species occurs in a single isolated station at Gwynn's bluff, Winona Co., Minn.; it is widespread in the Cordilleras.

13. *Potentilla tridentata*.—Collected by Rosendahl at Spring Grove, near Caledonia, Houston Co., Minn.; widespread under arctic-alpine and subarctic-subalpine conditions, although I have collected it as far south as Brasstown Bald in northern Georgia.

14. *Cornus canadensis*.—In balsam grove near Wykoff, Fillmore Co., and near Spring Grove, Minn.

15. *Taxus canadensis*.—Widespread on the cold bluffs in Iowa, Wis., and Minnesota; recurring more commonly along the shore region of Lake Superior; see Fassett, 1930.

16. *Pinus banksiana*.—In the "driftless" of Minnesota and of Wisconsin (see Fassett, 1930); the species is frequent at Whitewater State Park, Winona Co., Minn.

17. *Abies balsamea*.—In several stations in Iowa (see Conard, 1938), one in the "driftless" of Minnesota (west of Wykoff, Fillmore Co.), and at the Dells of the Wisconsin R., in Wisconsin. (See Fassett, 1930).

18. *Thuja occidentalis*.—In an isolated station at Gwynn's Bluff, Winona Co., Minn., where it is common.

19-20. *Betula papyrifera* and *Betula cordifolia*.—Local in the "driftless," in N. E. Iowa, S. E. Minnesota, S. W. Wisconsin.

21. *Acer spicatum*.—Infrequent in the "driftless" (see Fassett, 1930).

22. *Sullivantia renifolia*.—See Rosendahl (1927); not really a boreal but essentially a species of "cordilleran" relationships.

23. *Pyrus dumosa* = *subvestita*.—On bluffs in the "driftless area" (see Fassett, 1947).

24. *Primula mistassinica*.—Rare in the "driftless area" of Wisconsin (see Fassett, 1947), and in isolated stations in the putative migration route northward (as at 3 miles N. of Stillwater, Minn., where it is common), also in the "driftless area" in northern Illinois and in Iowa. (Personal communication from Dr. H. S. Conard: the species is now extinct in Iowa).

25. *Woodsia cathcartiana-oregana* complex.—Scattered in the "driftless"; again around the periphery of Lake Superior (in Cook Co.), but essentially "cordilleran" in distribution.

26. *Equisetum scirpoides*.—In the "driftless area" in Minnesota.

27. *Lycopodium obscurum* and var. *dendroideum*.—In Wisconsin south to Sauk, Adams, Juneau counties. (i.e., in the "driftless area") Wilson (1930); also at Gwynn's Bluff, Minn. (Rosendahl).

28. *Lycopodium tristachyum*.—In Wisconsin south to Sauk and Marquette counties (Wilson, 1930).

29. *Populus balsamifera*.—The writer has found four single trees of this species on the Sugar Loaf, near Winona, Winona County, Minn. (It recurs again in scattered sites north of the "driftless area," as at the Apple River, Wis.).

30. *Solidago hispida* var. *arnoglossa*.—A subarctic-subalpine species occurring in the "driftless area" (Houston Co., Minn.; see Rosendahl and Cronquist (1945).

There are, in addition, a rather large number of species which occur as relict colonies slightly to the north of the "driftless," and which recur more commonly around the periphery of Lake Superior. These species, like most of those in the above list, are restricted largely to moist, cold, often basic sandstone and limestone cliff walls. Among them are such species as:

1. *Thuja occidentalis, Abies balsamea, Mitella nuda, Pyrola secunda, Taxus canadensis, Pinus banksiana, Equisetum scirpoides*.—At Apple River, near Somerset, Wis.

2. *Streptopus amplexifolius* var. *denticulatus*.—At Taylors Falls on the Wisconsin side of the St. Croix R. (Schuster). (Fassett, 1935, restricts this in occurrence to the Lake Superior shore, in our region.)

3. *Lycopodium selago* var. *patens*.—On cliff at Ft. Snelling, Minneapolis, Minn. (Rosendahl).

4. *Primula mistassinica*.—In valley of St. Croix R., 3 miles north of Stillwater, Minn. I have found the species common here.

5. *Potentilla fruticosa*.—Near Savage, Dakota Co., Minn., in the valley of the Minnesota R.

6. *Viola adunca* var. *glabra*.—In an isolated station (together with such northern Hepaticae as *Tritomaria quinquedentata, Lophozia barbata*, etc.) at Taylors Fall, Wis.

The above list of boreal species, occurring in the Minnesota, Mississippi, Wisconsin, and St. Croix river basins, *northward* from the "driftless area," could be multiplied almost indefinitely. The occurrence of these species there today is significant, for the following reasons:

1. The area to the north was glaciated (therefore their occurrence northward is postglacial).

2. Since the end of the Wisconsin Glaciation, climatic conditions have apparently not been favorable for a *southward* migration of northern species, especially during and since the climatic optimum; hence these boreal elements in the region peripheral to the "driftless area" could scarcely have migrated southward from the Lake Superior area, where they are relatively common.

3. It is therefore possible that these species represent relict colonies, scattered along the obvious migration paths which these (and probably countless other) species followed in their postglacial migration northward, from the "driftless area."

This migration route is indicated not only for boreal species, but also for other, more eastern types, such as *Tsuga canadensis*. Fassett (1930) reports this from the "driftless area" in Wisconsin (Dane, Iowa, Vernon counties). The isolated stations of *Tsuga* near the western periphery, at Taylors Falls, Minn. (C. O. Rosendahl in personal conversation), and south of Duluth, and at Mille Lacs Lake cannot be easily explained, since they occur in a region that was fully glaciated. Their occurrence there today is evidently postglacial. The closest unglaciated point from which the species could have migrated, and in which it could have survived the last glaciation, is in the "driftless area."

In addition to such circumstantial evidence, we have a little more direct evidence for the nature of the bryophyte flora of the area fringing the "driftless area" during the Pleistocene. Holzinger (1903) described, from peat underneath the Kansan Drift (32 feet below the surface of the ground) near Oelwein, Iowa, such boreal mosses as *Drepanocladus fluitans, D. brachydictyus, D. revolvens, Calliergon Richardsoni,* as well as *D. fluitans glaciale,* from beneath 18 feet at Iowa City. The occurrence of such "boreal" mosses in the region during the Pleistocene is *prima facie* evidence that elements of a boreal moss flora existed there then, that do not exist there now. Even better evidence is offered by the study of Steere (1941) of the Aftonian interglacial deposits of Iowa, in which he found such northern species no longer present in Iowa today as *Sphagnum squarrosum, Dicranum bergeri, Calliergon stramineum, C. cordifolium, C. Richardsoni, C. giganteum, C. trifarium, C. turgescens, Drepanocladus exannulatus, Scorpidium scorpioides* (common now in marl bogs of N. E. Minnesota!), *Camptothecium nitens, C. woldenii, Polytrichum strictum* (common in N. E. Minnesota today!). In addition, some species were found that still occur in Iowa today (such as *Leptodictyum riparium, Campylium stellatum, Hylocomium splendens, Anomodon attenuatus,* etc.). We get, from such studies, the general picture of a widespread boreal flora in that region, during at least parts of the Pleistocene, of which today only few remnants survive. There is no reason that the vascular plants which occur in N. E. Minnesota and N. Wisconsin and Michigan (together with the mosses enumerated above), should not only have occurred to the south, in

and at the periphery of the "driftless area," during the time of maximum Pleistocene glaciation, but also persisted (in part) during the cool interglacial periods (e.g., between the advance of the Nebraskan and Kansan ice sheets).

The above examples, which could be multiplied by further literature work, are cited to show that the "driftless region," though it unquestionably served as a refugium for southern and Appalachian species (as Fassett develops, 1931), also appears to have served as a refugium for boreal and arctic-alpine elements.* Some of these still survive in pockets there (*Mannia pilosa, Clevea, Asterella saccata, Frullania bolanderi,* etc.); others have migrated northward partially, but left colonies in the glaciated area to the north, in ravines and on bluffs in the cold east-west running cuts in the Mississippi and St. Croix valleys (such as *Primula mistassinica, Mitella nuda, Streptopus amplexifolius* var. *denticulatus, Thuja occidentalis, Potentilla fruticulosa, Abies balsamea, Lycopodium selago,* etc.).

Fassett (1931) states that the "relic flora in the 'driftless area' . . . has its affinities mostly with regions south of the area of Wisconsin glaciation." However, even Fassett emphasizes that there is a decided Canadian and Hudsonian element in the "driftless area," including plants such as "*Arctostaphylos Uva-ursi* var. *coactilis, Moneses uniflora, Equisetum scirpoides, Pyrus dumosa . . . Pinus banksiana, Acer spicatum, Primula mistassinica* and *Rhododendron lapponicum. . . .*" Fassett goes on then to state: "It is hard to conceive of *Rubus parviflorus. . . . Arenaria macrophylla, Epipactis decipiens, Osmorhiza divaricata, Viola adunca* var. *glabra,* and *Potamogeton filiformis* var. *Macounii* . . . as having migrated northward in a body, leaving no traces, from a region where on some exposed bluffs and damp walls of canyons we know such Canadian and Hudsonian plants [such as those listed above]."

This argument, to the writer, lacks validity. Just because some subarctic and arctic-alpine species, listed previously, have left colonies behind (either in the "driftless" itself, or somewhat to its north, in the presumed northward route of migration) does not mean that *all* of the boreal or arctic species should have left traces or relict colonies in the "driftless." If then, the most striking of the arctic-alpine species, such as *Empetrum nigrum, Selaginella selaginoides, Sagina nodosa, Scirpus cespitosus* (and others among the vascular plants) are lacking, as well as the species listed by Fassett, this is certainly no cause for surprise, nor for concluding that the "driftless area" could not have served as a Pleistocene refugium for these species.

Furthermore, as has been pointed out, at least a portion of the species (such as *Empetrum, Selaginella selaginoides,* and many others), are today confined to the extreme margins of the cold waters of Lake Superior — to a real, edaphically and microclimatically controlled tundra zone. Such species, with such a restricted distribution, able to hold their own today in only a narrow zone kept cold by the frigid waters of Lake Superior, can scarcely be

* When one considers that at Whitewater State Park, Winona Co., Minn., there occur together (in a very small area) arctic-alpine forms such as *Mannia sibirica,* Appalachian species such as *Jeffersonia diphylla,* a Mississippi Valley species such as *Hydrophyllum appendiculatum,* species such as *Frullania bolanderi,* characteristic of the Pacific Coast, and prairie species, such as *Lithospermum canescens* and *Anemone patens,* the extraordinarily synthetic nature of the flora of the "driftless area" and its periphery can scarcely escape one.

expected to have held their own during the postglacial climatic optimum in the "driftless area." Their present absence from the latter, therefore, is to be expected, even if they at one time inhabited it.

Therefore the statement by Fassett (1931, p. 228) that "the occurrence in the Lake Superior region of plants of the Rocky Mountains and of the Gulf of St. Lawrence area is a problem that cannot at present be solved with any degree of certainty" is explicable only if one wholly rejects, as did Fassett, the possibility of the "driftless area" as a Pleistocene "refugium" for elements of the boreal flora. Although we have seen that there are very few "cordilleran" flowering plants recurring in the "driftless area," in the Lake Superior area, and again in the St. Lawrence, there are several species of Hepaticae that tie the "driftless area" in with this "cordilleran" and St. Lawrence distribution pattern. These are essentially *Frullania bolanderi, Asterella saccata, Mannia pilosa* and *Clevea hyalina.* All of these, except *Asterella saccata,* occur in the Gaspé, occur again in the Cordilleras (or along the Pacific Coast), and recur again in the Great Lakes area (except the *Clevea*). The ranges of such species as *Frullania bolanderi* and *Mannia pilosa,* therefore, suggest that the "driftless area" is probably a valid "refugium," in which some of the "critical" species of restricted range were able to find shelter during the Pleistocene. Furthermore, if the area was large enough, with a great enough diversity of sites, to shelter types as different in their requirements as *Clevea hyalina, Mertensia paniculata, Asterella saccata, Chrysosplenium iowense,* it conceivably may have provided sites suitable for such woody Lake Superior disjuncts as *Rubus parviflorus* and *Oplopanax horridus.* Until an explanation of how these latter two species were able to shift rapidly from one site to the next, along a "periglacial boundary" (from which they are notably absent today!) is forthcoming, the writer prefers to believe that the above explanation of the present range seems more reasonable. Such an explanation would assume that these species were present in suitable habitats in the general region lying to the north of the "driftless area" in the immediate pre-Pleistocene period, and are, therefore, "critical" species in the strict sense.

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Hybridity in the Verbenaceae

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Because of the considerable current interest in cytology, genetics, and plant breeding and also because of the very considerable horticultural value of the group, it has been thought advisable to bring together in one brief paper notes on the natural and artificial hybrids currently known or thought to exist in the Verbenaceae. This plant family, consisting of 90 genera and 3318 specific and subspecific entities, according to the latest count, is noteworthy in the number of supposed hybrids included in its ranks.

Over the past 27 years during which I have worked monographically on this group quite a few specimens of these hybrid forms have passed through my hands. These specimens are listed here so that persons especially interested in the subject, either from the cytologic, genetic, or horticultural point of view, will know where they may be found for examination and comparison. Synonymy, common names, habitat notes, time of blooming and fruiting, misidentifications in herbaria, and other relevant notes are also included.

It seems to me very likely that there exist many more natural hybrids in the group than have to date been described, possibly accounting, in part, at least, for the tremendous morphological "variation" observed in so many of the commoner species as represented in herbaria. Members of the group are all insect-pollinated and many genera are notable for their very showy flowers, which often, according to field workers' observations, attract "hordes of insects." In many genera the described species are obviously very closely related, often grow side by side, and frequently bloom contemporaneously. It would seem very probable that insects would often carry pollen from the flowers of one species to those of another, especially where, as in *Aegiphila, Callicarpa, Lantana, Lippia, Amasonia, Phyla,* etc., the species are so often distinguished more by habitat, foliar, and fruit differences and the flowers are very similar in appearance.

It seems almost inconceivable, for instance, that the ten very similar species of *Aegiphila* growing on the island of Jamaica should not hybridize there, especially the seven endemic montane ones. It seems equally probable that *A. integrifolia, A. sellowiana,* and *A. guianensis* hybridize where their ranges overlap. Some taxa in this relationship, hitherto given specific rank, may actually represent some of these hybrids, and some of the puzzling "intermediate forms" which cause us to describe the species as "variable" may also represent hybrids. This is almost certainly true in the *Aloysia lycioides* complex, where no hybrids have been described, but where various "species" and "varieties" have been described and are currently accepted, but are often difficult to separate where their natural ranges overlap.

Where several species of *Avicennia* — in the related family *Avicenniaceae*

— grow together in the definitely circumscribed ecological formation of mangrove swamp, it seems almost unbelievable that they would not at least sometimes hybridize. No such hybrids have been named as yet, but most of the species are described as being "very polymorphic" — a condition which, when observed in closely related species with overlapping range, similar habitat, similar general habit, similar flowers, and contemporaneous anthesis, leads one to suspect the presence of possible hybridity.

The members of the genus *Amasonia* are all very similar in general habit. Most of them are regarded as exasperatingly "polymorphic," "variable," or "intergrading," and they often occupy the same or contiguous regions in tropical South America. Certain species of the very showy-flowered genus *Petrea* — like *P. bracteata*, for instance — also show tremendous variability. Hybridity may be involved here, and it is almost certain that *Verbena bonariensis*, *V. brasiliensis*, *V. litoralis*, and *V. isabellei* interbreed where they grow together. No such hybrids have as yet been segregated, but they surely exist and are probably well-represented among the scores of more or less intermediate, often poorly fruited, specimens found in all major herbaria under one specific name or the other. It may well be that some of the many scientific binomials, trinomials, and quadrinomials currently reduced to synonymy under some of these species actually represent hybrid forms.

It seems obvious that interbreeding plays an important part in the complexity and nomenclatural difficulties encountered in the genus *Phyla*. The variability in what is regarded today as *P. incisa*, for instance, certainly does not appear to be "normal." Surely *Lantana camara* and its many-named varieties interbreed readily. It probably interbreeds also with such related species as *L. arida*, *L. ovatifolia*, *L. bahamensis*, *L. moritziana*, *L. armata*, etc., where the opportunity for so doing presents itself. The same is probably true of *L. balansae* and *L. montevidensis* in Argentina, Paraguay, and Uruguay, and with *L. involucrata* and *L. reticulata* in the West Indies. Some of the endemic "species" in this affinity, found in the Greater Antilles, may represent such hybrids.

It seems to me not at all impossible that the so-called "intermediate" specimens which have caused *Petitia poeppigii* to be reduced to synonymy under *P. domingensis* actually represent a hybrid between two valid species. I also suspect that what is passing as *Stachytarpheta australis* var. *neocaledonica* may be a hybrid with *S. urticaefolia* as one "parent." It seems rather certain, moreover, that *Perkins* 419 represents an as yet unnamed natural hybrid between *Citharexylum caudatum* and *C. fruticosum*, while the same collector's no. 1320 represents an as yet undescribed hybrid between *C. caudatum* and *C. spinosum*.

On the other hand, the supposed hybrid between *Stachytarpheta indica* and *Svensonia hyderobadensis* referred to by Moldenke (1936) is actually not of hybrid origin at all, but represents what is currently known as *Stachytarpheta jamaicensis* f. *monstrosa*, supposed to be caused by systemic infection of the plant by the sandal spike disease virus, *Chlorogenus santali* Holmes.

The 92 different symbolic abbreviations for the names of the herbaria

in which the specimens cited below are deposited are all fully explained by Moldenke (1955a). They can easily be consulted there by anyone interested and so, to conserve space, they are not repeated here. Where more than one specimen of a given collection is represented in a single herbarium, this fact is indicated below by a phrase after the herbarium symbol. Thus, "Bz—2 sheets" means that two specimens of the same collection are in the Herbarium Bogoriense at Buitenzorg, and "N—10 sheets" indicates the presence of no less than ten sheets of the same collection in the Britton Herbarium at the New York Botanical Garden. Several specimens of the same collection in a single herbarium certainly help workers there to see the variability or lack of variability in a given taxon, but in this nuclear age it would seem most reprehensible for curators of herbaria to keep more than one sheet of a collection under one roof. Wide distribution of duplicates, among other herbaria may result in at least one specimen being preserved intact for posterity!

xCALLICARPA SHIRASAWANA

This binomial was applied by Makino (1910) to a supposed natural hybrid between *C. japonica* Thunb. and *C. mollis* Sieb. & Zucc. It is the "*Callicarpa mollis*" of Shirasawa (1907). It is referred to also by Matsumura (1912), Nakai (1927, 1938), Rehder (1940, 1949), Hara (1948), and Moldenke (1940, 1942a and b, 1949). Moldenke (1936) gives it in the synonymy of *C. mollis*. It is the "*Callicarpa mollis* x *japonica*" of Schneider (1911). The so-called "*Callicarpa shirasawana*" of horticulture is (insofar as observed by me) nothing more nor less than typical *C. japonica*.

xCARYOPTERIS CLANDONENSIS

Simmonds (1933) proposed this name for a chance hybrid between *C. incana* (Thunb.) Miq. and *C. mongholica* Bunge. It is described and illustrated again by A. T. Johnson (1942) and is described by or referred to by Anon. (1934), Rehder (1940, 1949, 1954), Turrill (1949), Salisbury (1953) and Moldenke (1941, 1942, 1942a, 1949). Synonymous designations are *Caryopteris clandonensis* Hort. ex Moldenke (1939) and *C. mastacanthus* var. *clandonensis* Anon. (1941).

The hybrid was cultivated by Simmonds, who was then assistant secretary of the Royal Horticultural Society, at West Clandon, Surrey, England. The corolla-color is described as "blue dauphin, near 203 .f .l of Rép. Coulour." Moldenke's specimen cited below is actually a topotype.

Material examined.—CULTIVATED. ENGLAND: *Moldenke & Moldenke* 9268 (N); *Musgrove s.n.* [September 1936] (N). MASSACHUSETTS: *E. J. Palmer s.n.* [Herb. Arnold Arb. 526-36] (Ur); *Wilberding* 562-36 [Aug. 18, 1936] (Ba), 562-36 [Oct. 22, 1936] (Ba).

xCITHAREXYLUM HYBRIDUM

This binomial was proposed by Moldenke (1939a) for a series of specimens tentatively placed in *C. spinosum* L., but which seem more or less intermediate between that species and *C. fruticosum* L. Typical material of both

species is very common in the Lesser Antilles, but most of the specimens from the southern extreme of their range — that is, from Saint Vincent, Grenada, Trinidad, Tobago, Venezuela, and the Guianas seem different from both and may represent a natural hybrid between the two species. The supposed hybrid is well represented by *W. E. Broadway* 955 (B—2 sheets), 4064 (B, F), 4065 (N—type), and 6658 (Bm, E, F, Ms—2 sheets, W), *Eggers* 5484 (B, K), *Sandwith* 1821 (N), and *Smith & Smith* 405 (B, Ed, G). The hybrid seems to show a predominance of *C. spinosum* characters—e.g., the long-stalked flowers as seen on the Chicago Natural History specimen of *Broadway* 6658—and so is most usually identified in herbaria as that species.

LANTANA NOTHA

This binomial was proposed by Moldenke (1940b) for what was then regarded as a natural species from Sinaloa, Mexico. There is no evidence that it is of hybrid origin. The placing of an "x"—as the sign of a hybrid—before the binomial by Moldenke (1942a, 1949) was apparently an inadvertent typographic error perpetuated by copying.

xLANTANA SCORTA

Moldenke (1940a) proposed this binomial without any definite hybrid designation. It was listed earlier as a hyponym (Moldenke, 1939b). In the original discussion, however, it was pointed out that plants so designated probably represent a natural hybrid between *L. horrida* H.B.K. and *L. glandulosissima* Hayek, with perhaps *L. hirsuta* Mart. & Gal. (now called *L. hispida* H.B.K.) also involved. The true *L. camara* L. is probably not involved in its immediate ancestry because of its relative scarcity in Mexico. Study of a large series of herbarium specimens indicates that, in general, the northernmost specimens in Mexico are typical *L. horrida*, those from the West Indies are typical *L. camara* and its several named varieties, those from around Mount Orizaba in Veracruz are typical *L. hispida*, and those from central and southern Central America are typical *L. glandulosissima*. In central Mexico and the Yucatán Peninsula, however, plants occur very abundantly which do not fit well into any of these specific categories and which show combinations in various strengths of the characters of two or three of these species. It seems to me that we do not have here one extremely widespread and polymorphic species ("*L. camara*") as some might be led to suppose on the basis of superficial examination of a small amount of material, but, rather, that we have at least four distinct but closely related species, which are more or less fertile to each other's pollen and have therefore, because of this fact and their overlapping geographic range and very similar and showy entomophilous flowers, freely crossed and hybridized. For convenience in reference, it seems to me that a binomial name like *L. scorta* to designate such hybrid populations is highly desirable, even though the characters of such a "hybrid species" will of necessity be extremely elastic and will merge completely on the one hand into those of one "parent" and on the other hand into those of the other "parent" form. It is certainly preferable

to such a long and cumbersome designation as, for instance, "*L. glandulosissima* x *horrida* x *hispida*," as some students might propose, for, in addition to its awkwardness, the latter would imply a certain knowledge of the plant's exact parentage. In the present and in other cases in this family we do not have any such definite knowledge. Use of a binomial for hybrid populations also makes for permanence in nomenclature, for such a name would remain the same no matter how often the accepted name of either "parent" changes.

The *Lundell & Lundell* 8205 and *Steere* 3025 cited below represent a very small-leaved form. The corolla of x*L. scorta* is variously described by collectors as orange, orange-red, and red, and it has been collected in anthesis from March to December and in fruit from May to December. Hinton records the common names "yerba de tres colores" and "frutilla parar comer." Miss Mexia records the names "lantana" and "frutilla," Bárcena records "siete colores," and Rovirosa lists "cinco-negritos" and "palabra-de-muger." It has been collected in moist open places, low second growth, cactus thickets, and old clearings, along trailsides, on hills, banks, dry hillsides, rolling prairies, and open ground, and in arroyos, moist or wooded montane ravines, llanos, pine forests, barrancas, and palm-oak canyons, at altitudes of from 32 to 2205 meters.

Material examined.—MEXICO. CHIHUAHUA: *H. S. Gentry* 2869 (Oa); *LeSueur* 1197 (Au, Gg). COLIMA: *N. L. H. Krauss* 258 (Hk). FEDERAL DISTRICT: *Lyonnet* 212 (N); *Reiche s.n.* [VI. 14] (Me). HIDALGO: *V. H. Chase* 7214 (Fs, Ld, N, Ur); *Matuda* 18861 (N). JALISCO: *J. T. Howell* 10301 (Po); *M. E. Jones* 359 (Po), 360 (Po), 416 (Po); *Edw. Palmer* 221 (Pa), 400 (Me); *Pringle* 2908 (Vt), 4481 (Br, C, Me-3 sheets, Mi, Ob, S, Vt), 9345 (It, La, N, Vt). MÉXICO: *Bárcena* 396 (Me); *Hinton* 1058 (N-2 sheets), 1233 (N-2 sheets), 5357 (N-2 sheets), 6366 (N), 6373 (N), 6829 (N). MICHOACÁN: *Hinton* 12033 (N), 13005 (N-2 sheets), 13852 (N); *Hitchcock & Stanford* 7155 (W); *N. L. H. Krauss* 256 (Hk). MORELOS: *Rose & Rose* 11063 (N). NAYARIT: *Bravo Hollis* 253-7144 (Me); *R. J. Ferris* 5799 (Du), 5908 (Du); *M. E. Jones* 23237 (En); *Mexia* 595 (Mi); *Rose, Standley, & Russell* 14335 (N). NUEVO LEON: *Mueller & Mueller* 163 (Me); *F. W. Pennell* 16907 (W). OAXACA: *Galeotti* 795c (Br-2 sheets); *Morton & Makrinius* 2602 (Du); *Webster, Rowell, & Barkley* 17M376 (N). PUEBLA: *Arsène* 2210 (N); *Nicolas* 5426 (N), 6103 (Ba, Br, N, S, Ur), *s.n.* [15/9/1900] (Br), *s.n.* [Cholula prés Puebla, 15/9/1910] (Bz, N-2 sheets). QUERÉTARO: *Rose, Painter, & Rose* 9520 (Me-isotype, N-type). QUINTANA ROO: *G. F. Gaumer* 2004 (Br, Du, F); *Lundell & Lundell* 7672 (Mi, N); *Steere* 2941 (Mi). SAN LUIS POTOSÍ: *V. H. Chase* 7528 (N, Ur); *Frye & Frye* 2961 (Pl, Se); *N. L. H. Krauss* 269 (Hk); *J. Mann* 17 (Mi, N, W, Z); *Yates & Wilcox* 8 (Ak). SINALOA: *Lamb* 360a (Du). SONORA: *H. S. Gentry* 744 (Du); *Rose, Standley, & Russell* 12933 (N). TABASCO: *E. P. Johnson s.n.* (C); *N. L. H. Krauss* 253 (Hk); *J. N. Rovirosa* 370 (Pa). TAMAULIPAS: *J. Mann* 16 (Ca, Cb, G, Hk, K, Mi, N, S, W). VERACRUZ: *N. L. H. Krauss* 279 (Hk); *MacDaniels* 819 (Ba); *J. Mann* 13, in part (Cb). YUCATÁN: *G. F. Gaumer* 508, in part (Br, Gg, N), 1971 (F); *N. L. H. Krauss* 249 (Hk); *Lundell & Lundell* 7401 (Mi, N); 8205 (Mi, N); *Steere* 3025 (F). STATE UNDETERMINED: *B. J. Bayer s.n.* (Bj); *R. E. Griffith* 84, in part (T); *Herb. Calif. Acad. Sci.* 31120 [Herb. Prager 18649, in part] (Gg). LOCALITY UNDESIGNATED (presumably Mexico): *Berlandier* 790 (S); *Martinis s.n.* (Br).

xSTACHYTARPHETA ABORTIVA

This name was proposed by Danser (1929) for the hybrid which he produced artificially between what he regarded as *S. cayennensis* (L. C. Rich.)

Vahl (but which was actually *S. australis* Moldenke) and *S. mutabilis* (Jacq.) Vahl. When he described it he stated that it had not yet been found in the wild. Since then a specimen collected in the Seychelles Islands in 1876 has been found which seems to be this same hybrid, and several specimens collected on the island of Java may have been from wild material for their labels do not indicate that they were taken from cultivated material. A specimen from the Singapore Botanical Garden, there cultivated as "*Stachytarpheta rosea*," may or may not have been from Danser's original stock. Its flowers are described as rose-pink or red-pink and it is said to grow 4 feet tall there. Koppel describes the flower of his plant, cited below, as violet.

Danser, in his original description, states that he never saw the flowers of this hybrid. He states that he was not successful when he placed *S. australis* pollen on the stigmas of *S. mutabilis*, but he secured 200 seeds when he made the reciprocal cross. Of 98 plants produced from these seeds, 94 were typical *S. australis* and the other 4 were x*S. abortiva*.

Material examined.—JAVA: *Bakhuizen van den Brink* 7639 (Bz); *Koppel s.n.* [2 Jan. 1931] (Bz), *s.n.* [14 Maart 1931] (Bz). SEYCHELLES ISLANDS: *Herb. Mus. Paris s.n.* [Mars 1876] (Br). CULTIVATED. JAVA: *Bakhuizen van den Brink* 7587 (Bz-cotype), 7594 (Bz-cotype); *Danser* 6818 (Bz-cotype), 6904 (Bz-3 cotypes, N-cotype, N-photo of cotype, Ut-cotype, Z-photo of cotype). SINGAPORE: *Clemens & Clemens* 22568 [field no. 8010] (N).

xSTACHYTARPHETA ADULTERINA

Urban & Ekman (1929) proposed this binomial for the natural hybrid between *S. jamaicensis* (L.) Vahl and *S. mutabilis* (Jacq.) Vahl, which Britton (1910) had merely indicated as "*Valerianodes jamaicensis* x *mutabilis*," and the type of which was collected by him "among the parents" along roadside between Mandeville and Brown's Town, Manchester, Jamaica.

Danser (1929) described the same hybrid, but unfortunately used the name x*S. trimeni* Rech. for it. Both Danser and Rechinger regarded their respective plants as hybrids between "*S. indica*" and *S. mutabilis* and so designated them. However, Rechinger's "*S. indica*" was *S. urticaefolia* (Salisb.) Sims, while Danser's was *S. jamaicensis*. Danser's plant, therefore, was not x*S. trimeni*, but was x*S. adulterina* of Urban & Ekman.

Misled by this confusion of names, Moldenke (1941, 1942b) stated that "*Stachytarpheta indica* x *mutabilis* Dans." is x*S. trimeni* and that *S. speciosa* Dans. is x*S. adulterina*. Actually, the former is x*S. adulterina* and the latter is x*S. trimeni*.

Danser gives a very detailed description of the morphological characters of this hybrid, which, he says, has the height of *S. mutabilis*, but the general facies of *S. jamaicensis*. He notes that the description of Rechinger's plant does not agree in all particulars with his plant, but that the curators of the Rechinger Herbarium at Vienna regarded both plants as the same when he sent some material of his plant to them. Danser never found x*S. adulterina* wild; he produced his plants by artificial pollination in 1926. He predicts, however, that this hybrid will be found where cultivated specimens of *S. mutabilis* grow in proximity to wild material of *S. jamaicensis*. He secured

no fruit when he pollinated *S. mutabilis* pistils with *S. jamaicensis* pollen, but the reciprocal cross was very successful, yielding 30 plants. Of these, 14 were typical *S. jamaicensis* and 16 were the hybrid. He describes the corolla of the hybrid as violet, darker and reddish toward the throat and lighter at the edges. Ekman describes the flowers as "always some shade of violet" or "purple-violet"; Leonard calls them "bright purple" or "dark bright purple"; Chrysler calls them "medium-blue"; and Nash & Taylor say they are "purple."

Although in Java it is apparently known only from cultivated material, plants that were presumably wild have been found on Sumatra, Mahé, Jamaica, and Haiti. In Haiti it has been found in open grassy places on mountain tops, on eruptive hills, and along roadsides at altitudes of 350 to 1200 meters, blooming and fruiting in May, August, September, and November, and is said to be a shrubby plant from 2 feet to 1 meter tall. In Jamaica it was collected in anthesis in June, growing in open ground near a roadside.

It is listed by Moldenke (1942a, 1949).

Material examined.—JAMAICA: *Chrysler* 1527 (Ru), 4740 (N, Ru). HAITI: *Ekman H.*2482 (F, Mi, S, W), *H.*4898 (S, W), *H.*6113 (S); *E. C. Leonard* 7596 (N, W); *Nash & Taylor* 1707 (N). SEYCHELLES ISLANDS: MAHÉ: *L'Isle s.n.* [Mars 1876] (P). SUMATRA: *Huitema* 67 (Bz, N). CULTIVATED. JAVA: *Danser* 6665 (Br, Bz-3 sheets, N-photo, Z-photo).

xSTACHYTARPHETA GRACILIS

This name was proposed by Danser (1929) for the natural hybrid between his "*S. cayennensis* (L. C. Rich.) Vahl" [actually *S. australis* Moldenke] and what he calls "*S. jamaicensis* (L.) Vahl" [actually *S. urticaefolia* (Salisb.) Sims]. He based the name on eight of his own and three of Bakhuizen van den Brink's collections, and says that the hybrid is not at all uncommon where both "parents" grow in large quantities. The color of the corolla, he says, is rather dark blue-violet, most like that of *S. urticaefolia*, but slightly lighter. Actually, x*S. gracilis* looks most like a small-flowered, small-leaved, and in all respects more slender form of *S. urticaefolia*, with thin inflorescence-rachis. It is also known from Oahu, and is mentioned by Moldenke (1941, 1942a and b, 1949).

Material examined.—JAVA: *Bakhuizen van den Brink* 5389 (Bz-2 cotypes, Ut-cotype), 5390 (Bz-2 cotypes), 5409 (Bz-cotype); *Bakhuizen van den Brink Jr.* 1077 (Ut); *Danser* 6398 (Bz-2 cotypes, N-cotype), 6399 (Bz-2 cotypes), 6407 (Bz-cotype), 6424 (Bz-cotype, N-photo of cotype, Ut-cotype, Z-photo of cotype), 6425 (Bz-cotype), 6657 (Bz-cotype), 6658 (Bz-cotype), 6659 (Bz-cotype); *Van Steenis* 247 (Bz). HAWAIIAN ISLANDS: OAHU: *S. W. Hutchinson* 6043 (B1).

xSTACHYTARPHETA DEBILIS

Danser (1929) proposed this name for the natural hybrid between *S. australis* Moldenke and *S. jamaicensis* (L.) Vahl, but which he called "*Stachytarpheta cayennensis* x *indica*." He stated that the hybrid is much more similar in habit and general appearance to *S. jamaicensis* than it is to

S. australis. This is not surprising since *S. jamaicensis* seems usually to be dominant in its hybrids. x*S. debilis* actually looks much like a weak, small-leaved, small- and pale-flowered specimen of *S. jamaicensis*. Its sterility points to its hybrid origin. It also possesses some *S. australis* characters, such as the less smooth leaf-blades, more abundant puberulence throughout, and more sculptured inflorescence-rachis. It is referred to by Moldenke (1941, 1942a and b, 1949).

Danser found this hybrid twice in the wild state at Buitenzorg, each time growing among its "parents." He transplanted one of these plants to his garden, where it grew to be a large but always low and more or less procumbent subshrub. He also found a plant of this hybrid among three plants secured from seed of *S. jamaicensis* planted by him in his garden.

Material examined.—JAVA: *Danser* 6400 (Bz-cotype, N-photo of cotype, Z-photo of cotype), 6819 (Bz-2 cotypes). CULTIVATED. JAVA: *Danser* 6656 (Bz, N).

xSTACHYTARPHETA HYBRIDA

This name was proposed by Moldenke (1940b) for the natural hybrid between *S. jamaicensis* (L.) Vahl and *S. strigosa* Vahl. It appears to be not uncommon in the Greater Antilles where its two "parents" grow together. It is usually identified in herbaria either as one or the other "parent." The corolla is described as "blue," "pale blue," "purple," or "dark purple." The plant has been found in pinelands, waste places, on hillsides, river terraces, and limestone areas, and "common along roadsides," flowering in February, March, July, October, November, and December. Ekman found it at an altitude of 1100 meters. It is referred to by Moldenke (1942a, 1949).

Material examined.—DOMINICAN REPUBLIC: *Ekman H.*11978 (N-isotype, N-photo of type, S-isotype, W-type, Z-photo of type), *H.*13187 (S), *H.*16011 (S). PUERTO RICO: *Britton & Britton* 9595 (N); *Britton, Britton, & Brown* 6067 (N); *Goll* 743 (W); *Sintenis* 2380 (Io, S); *Taylor & Taylor s.n.* [Fort Cristobal, Oct. 1916] (Up). CULEBRITA ISLAND: *Britton & Wheeler* 276 (N, W). CULTIVATED. ITALY: *Herb. Harvey s.n.* [Hort. Bot. Neapol. 1812] (Du).

xSTACHYTARPHETA INTERCEDENS

When Danser (1929) proposed this name he regarded it as applying to the natural hybrid between "*S. indica*" and "*S. jamaicensis*." Actually, his "*S. indica*" is *S. jamaicensis* (L.) Vahl and what he calls "*S. jamaicensis*" is *S. urticaefolia* (Salisb.) Sims. He based the hybrid name on five of his own collections, two of Bakhuizen van den Brink, one of Beumée, and one of Backer, all from Java and apparently all taken from wild plants. He says that the hybrid is not at all uncommon at Buitenzorg where the two "parents" grow together in large numbers. He points out that many botanists have considerable difficulty in distinguishing the two "parent" species from each other. It goes almost without saying, therefore, that the hybrid, to the untrained eye, is still more difficult to detect. Yet where the plants grow reasonably separated and not too much intermingled one can pick out the hybrids and will notice that they resemble *S. jamaicensis* more closely than they do *S. urticaefolia*. In general, they have larger and darker flowers than

S. jamaicensis and are sterile. Some specimens which he studied gave evidence of being triple hybrids, with *S. australis* Moldenke [*"S. cayennensis"* of Danser] as the third "parent." Such plants have smaller flowers. Of nine such plants studied, seven were found to produce practically no pollen at all, while in the other two the pollen was only about one-third developed.

This hybrid is referred to by Moldenke (1941, 1942a and b, 1949).

Material examined.—JAVA: *Backer* 14405 (Bz-cotype); *Bakhuizen van den Brink* 5359 (Bz-3 cotypes), 6771 (Bz-2 cotypes, N-photo of cotype, Ut-cotype, Z-photo of cotype); *Beumée A.*614 (Bz-cotype), *A.*770 (Bz); *Danser* 6396 (Bz-cotype), 6397 (Bz-3 cotypes), 6660 (Bz-cotype), 6661 (Bz-2 cotypes, N-cotype, Ut-cotype), 6663 (Bz-2 cotypes); *Van Steenis* 2285 (Bz). LESSER SUNDA ISLANDS: BANKA: *Amand* 3 (Ut). CULTIVATED. JAVA: *Danser* 6662 (Bz, Ut).

xSTACHYTARPHETA TRIMENI

This name was originally proposed by Rechinger (1912) for the natural hybrid between *S. mutabilis* (Jacq.) Vahl and what he called *"S. indica"* [actually *S. urticaefolia* (Salisb.) Sims]. In 1929 Danser proposed the name x*Stachytarpheta speciosa* for the same hybrid. Danser, however, used the name *"S. jamaicensis"* for what was actually *S. urticaefolia.* He based his name on Backer's no. 31842, collected in 1909, and on Bakhuizen van den Brink's no. 5302, collected in 1921, both in the neighborhood of Buitenzorg. The latter collector transplanted his plants to the botanical garden at Buitenzorg and from them, says Danser, have been derived all the specimens seen and collected by Danser. Rechinger based his name on his no. 2285, collected near Kandy, Ceylon, growing among both "parents."

The hybrid is similar to *S. mutabilis* in its dark-green leaves and dark-violet corollas. Its showiness certainly makes it well worthy of further horticultural experimentation. It has a more slender, but stronger stem than does *S. mutabilis,* and with only a little pruning can be trained to form a small tree which will bloom profusely all year and make a splendid addition to the tropical garden. Its pollen is more fertile than one would expect from "parents" so different in appearance. Pistil fertility, however, is not as good —usually only two or three seeds are formed on an entire spike. From 150 seeds only 5 seedlings were secured. These were grown to maturity; they differed notably from each other, with the two sets of parental characters present in different degrees and combinations in each.

The hybrid is referred to by Moldenke (1941, 1942a and b, 1949).

Material examined.—JAVA: *Backer* 31842 (Bz-2 sheets, N-photo, Z-photo); *Bakhuizen van den Brink* 5302 (Bz-2 sheets), 7519 (Bz-3 sheets); *Bakhuizen van den Brink Jr.* 838 (Ut). MOLUCCA ISLANDS: AMBOINA: Rant 234 (Bz-2 sheets), 302 (Bz, N). CULTIVATED. JAVA: *Bakhuizen van den Brink* 6579 (Bz), 6581 (Br-2 sheets, Bz-7 sheets, F-photo, N-photo, Si-photo, Z-photo), 6588 (Bz); *Danser* 6664 (Br, Bz).

xVERBENA ADULTERINA

This name was first proposed by Haussknecht in Nyman (1889) without description. It is given again by Haussknecht (1897), where he says it is proposed for the natural hybrid between *Verbena officinalis* L. and *V. supina*

L. which he found growing wild among the parents in Greece. It is also listed by Durand and Jackson (1906). Most unfortunately, Hill, (1926) by mistake listed this epithet under the genus *Vitex* instead of *Verbena* and so the name "x*Vitex adulterina*" came into being. Not knowing of Haussknecht's x*Verbena adulterina* at the time, Moldenke (1955) proposed another "x*Verbena adulterina*" for the hybrid between *V. officinalis* and *V. halei*, now called x*V. conata*.

V. officinalis and *V. supina* grow together in many parts of Europe and the Orient, and the hybrid is certainly to be expected throughout that area. In fact, it may be that future study will reveal that some of the named "varieties" and "forms" of these two species may in actuality represent the hybrid instead.

xVERBENA BAILEYANA

Moldenke (1947) proposed this name for what appears to be a hybrid between *V. officinalis* L. and *V. hastata* L. The type was collected in the Jardin des Plantes at Paris in 1819, but it is not known if the hybrid appeared naturally or was artificially induced. Normally these two species would seldom be found growing in close proximity — one being European and the other North American. The former, however, has been introduced and grows as a weed in many parts of eastern North America where *V. hastata* grows naturally, and the latter is sometimes cultivated in Europe where *V. officinalis* is very common. The supposed hybrid shows a marked dominance of *V. hastata* characters. The Austrian specimen cited below does not bear any indication on its label that it came from cultivated material, but I assume that it did. Haartman (1756) actually produced this hybrid artificially and described it as "*Verbena hastata* x *spuria*." It is also referred to by Moldenke (1947a, 1949).

Material examined.—CULTIVATED. AUSTRIA: *Herb. Reichenbach f.* 160270 (N, V). FRANCE: *Herb. W. H. Harvey s.n.* [h.R.P. 1819] (Du-type, F-photo of type, N-photo of type, Z-photo of type).

xVERBENA BEALEI

This name was proposed by Moldenke (1946) for the hybrid between *V. hispida* Ruíz & Pav. and *V. litoralis* H.B.K. described by Dermen (1936). There is plenty of opportunity for this hybrid to occur in nature because the two parental species occupy the same geographic areas in Paraguay, in São Paulo, Brazil, and in at least three provinces of Bolivia, three of Chile, and ten of Argentina. It is very possible that some, at least, of the so-called puzzling forms of "*V. litoralis*" seen in herbaria represent this hybrid. This widespread species needs much more intensive study and when this is done possible hybridity should be kept in mind. The hybrid is referred to by Moldenke (1947a, 1949).

xVERBENA BINGENENSIS

Moldenke (1945) proposed this name for a supposed hybrid between *V. bracteata* Lag. & Rodr. and *V. lasiostachys* var. *septentrionalis* Moldenke.

The two "parents" grow together in at least nine counties of California, but thus far only one supposed parent, *V. bracteata,* has been seen by me from Klickitat County, Washington, where Suksdorf collected the type. This fact militates against the hypothetical second "parent," but possibly more intensive collecting may reveal its presence there. Suksdorf was a very intensive collector and one would suppose that he would have collected material of both "parents" if they occurred there in the bottomlands at Bingen in 1898 when he collected the type of the hybrid. The hybrid nature of this plant, therefore, and, if it is a hybrid, the exact identity of its second "parent," are still in doubt. It is referred to by Moldenke (1949).

Material examined.—WASHINGTON. KLICKITAT CO.: *Suksdorf s.n.* [July 9, 1898] (N-type, Pl-isotype).

xVERBENA BLANCHARDI

Moldenke (1937) proposed this name for the natural hybrid which occurs between *V. simplex* Lehm. and *V. hastata* L. where the ranges of these two species overlap in the eastern United States. The hybrid sometimes resembles one "parent," sometimes the other, in general habit. The leaves are generally broader, more acute, and with coarser pubescence and larger teeth than in *V. simplex,* more narrowly lanceolate or oblong-lanceolate than in *V. hastata* and never incised nor hastate. An illustration of a typical form of the hybrid is seen in Gleason (1952). Fruit is produced sparingly and irregularly, whereas in both "parents" fruit production is usually heavy. The hybrid is also referred to by Gates (1940), and Moldenke (1940, 1941, 1942b, 1944, 1947, 1949). Synonymous designations include the "*Verbena angustifolia* x *hastata*" of Blanchard and of Hill and the "*Verbena hastata* x *angustifolia*" of Hill. For a cytological discussion of the hybrid, see Kanda (1920).

Collectors report finding x*V. blanchardi* in dry fields and on roadside banks and railway rights of way, flowering and fruiting in June and August. They report the common names "blue vervain" and "false vervain." In herbaria it has been variously identified as *V. angustifolia* Michx., *V. hastata* L., *V. paniculata* Lam., and *V. rugosa* Willd. The corollas are described as "pale-blue" or "violet to lilac-blue." Gates states that it occurs in Butler, Cherokee, Douglas, Lyon, Montgomery, Neosho, and Orange counties, Kansas.

Material examined.—VERMONT. BENNINGTON CO.: *W. H. Blanchard* 162 (N). VIRGINIA. ROCKBRIDGE CO.: *Ruffner s.n.* (T-type). ILLINOIS. COOK CO.: *E. J. Hill* 161.1898 (Ur), *162.1898* (Ur-2 sheets). KENTUCKY. WARREN CO.: *S. N. Price s.n.* [Bowling Green, July 29, 1899] (N). OKLAHOMA. LATIMER CO.: *F. A. Barkley* 1219 (Ok), *s.n.* [6/20/28] (Ok). WAGONER CO.: *R. Bebb* 4324 (Ok). CULTIVATED. GERMANY: *Herb. Hort. Bot. Berol. s.n.* [1854] (N). LOCALITY OF COLLECTION UNDESIGNATED: *Collector undesignated* 43 (Q).

VERBENA BRACTEATA

MacDougal (1907) suggests that what he calls *V. bracteosa* Michx. (now more correctly known as *V. bracteata* Lag. & Rodr.) may hybridize in the wild with *V. canadensis* (L.) Britton, with *V. hastata* L., and with what

he calls *V. angustifolia* Michx. (now more correctly known as *V. simplex* Lehm.). However, he cites no specimens, gives no descriptions of the supposed hybrids, and does not say that he actually ever saw any such hybrid plants. I doubt very much whether these species hybridize and certainly have never yet seen any such hybrids myself.

VERBENA CANADENSIS

MacDougal (1907) suggests that *V. bracteosa* Michx. (now known as *V. bracteata* Lag. & Rodr.) may hybridize with *V. canadensis* (L.) Britton, but he cites no specimens, gives no description, and does not say that he actually saw any such hybrid. I doubt very much whether the hybrid exists.

xVERBENA CLEMENSORUM

This is a name proposed by Moldenke (1948) for the supposed natural hybrid between *V. officinalis* L. and *V. robusta* Greene. Both "parents" occur in Amador County, California, where the type was collected. They also occur in San Diego County and the hybrid may be expected there, too. Otherwise there seems little opportunity for the two species to come together in the wild state. *V. officinalis* is a European species, introduced and naturalized in some parts of the United States, while *V. robusta* is a species found only in California, the Channel Islands, and the Mexican state of Baja California. It is referred to by Moldenke (1949).

Material examined.—CALIFORNIA. AMADOR CO.: *M. K. Clemens s.n.* [Jackson, Sept. 13, 1920] (F-photo of type, Gg-type, N-isotype, N-photo of type, Si-photo of type, Z-photo of type).

x**Verbena conata**, nom. nov.

This name is hereby proposed for the hybrid between *V. officinalis* L. and *V. halei* Small, described by Dermen (1936) and named x*V. adulterina* by Moldenke (1955). Unfortunately, my name is invalidated by the earlier x*V. adulterina* Haussk. (Haussknecht, 1897), the existence of which I did not realize until now.

V. officinalis and *V. halei* grow together in Plaquemines Parish, Louisiana, but this is the only place I know of where the hybrid might occur in nature. It would be most difficult to recognize in the field because of the close similarity of the parents to each other. Lack of abundant fruit production would probably be the quickest and easiest way to locate it. Both *V. officinalis* and *V. halei* normally produce great quantities of fruit.

xVERBENA CORRUPTA

Moldenke (1955) proposed this name for the artificially produced hybrid between *V. peruviana* (L.) Britton and *V. phlogiflora* Cham. described by Schnack and Covas (1945) under the designation "*Glandularia peruviana* x *phlogiphlora*." The two parental species grow together in at least two states of Brazil, in Paraguay and Uruguay, and in at least two provinces of Argentina. It is quite probable that the hybrid occurs there in the natural

state. It should have considerable horticultural merit and should also be of interest in possibly shedding light on the supposed origin of the common garden verbena known as x*V. hybrida.*

xVERBENA COVASII

This name was proposed by Moldenke (1946) for the artificially produced hybrid between *V. santiaguensis* (Covas & Schnack) Moldenke and *V. laciniata* (L.) Briq., described by Schnack and Covas (1945, 1945a) under the name "*Glandularia santiaguensis* x *laciniata*." The two parental species grow together in at least two provinces of Argentina and the hybrid may be expected in the wild there. It should have considerable horticultural merit and therefore be worthy of further experimentation.

xVERBENA DEAMII

Moldenke (1937) proposed this name for the natural hybrid between *V. bracteata* Lag. & Rodr. and *V. stricta* Vent., commonly found where the ranges of the two species overlap in the central United States. It resembles *V. bracteata* in habit, but is stouter, with broad, laciniate, strongly reticulate leaves, larger flowers, smaller usually not foliaceous bractlets which are mostly about 5 mm long and are long-attenuate or -acuminate at the apex, the spikes usually only 6-10 mm wide and poorly fruited, and the pubescence in the inflorescence only softly villous. It is illustrated by Gleason (1952). Gates, (1940), records it from McPherson County, Kansas, while Palmer and Steyermark (1935), record it from Jasper County, Missouri. Synonymous designations include the "*Verbena stricta* x *bracteosa*" of Bebb, Eggert, Mackenzie, Rydberg, and Sandberg, the "*Verbena bracteata* x *stricta*" of Gates and of Palmer, and the *V. stricto-bracteosa* of Patterson. The so-called "*V. bracteata* x *stricta*" of Schneck, however, is x*V. perriana;* the "*V. bracteosa* x *stricta*" of Britton, Palmer, and Schneck is also x*V. perriana;* the "*V. bracteosa* x *stricta*" of Deam, Eggert, and Rydberg is x*V. rydbergii;* and the "*V. stricta* x *bracteosa*" of Hitchcock is x*V. perriana,* while that of Engberg is typical *V. bracteata.* The *V. stricto-bracteosa* of Engelmann is x*V. perriana.*

Collectors have found x*V. deamii* in copses, describe it as "decumbent," and have collected it in flower and fruit in June, July, and August. It is referred to by Moldenke (1940, 1942a and b, 1949).

Material examined.—ILLINOIS. HENDERSON CO.: *H. N. Patterson s.n.* [July 1872] (Al), *s.n.* [vicinity of Oquawka] (N, Ur). WABASH CO.: *Waite s.n.* [Mt. Carmel, Aug. 6, 1887] (Ur). IOWA. STORY CO.: *C. E. Bessey s.n.* [Ames, Aug. 23, 1878] (Ua). WISCONSIN. PIERCE CO.: *Schuette s.n.* [Bay Settlement, July 19, '83] (Du). MINNESOTA. HENNEPIN CO.: *Sandberg s.n.* [Aug. 1889] (Al, Up). KANSAS. RILEY CO.: *J. B. S. Norton s.n.* [Manhattan, Aug. 1892] (Ka). WYANDOTTE CO.: *Mackenzie s.n.* [Aug. 16, 1896] (N). NEBRASKA. BUFFALO CO.: *Rydberg s.n.* [Kearney, June 20, 1895] (N-type), *s.n.* [Kearney, June 1895] (N). MISSOURI. GREENE CO.: *Eggert s.n.* [Brookline, 13 July 1879] (Cm, N). SAINT LOUIS CO.: *Eggert 5321* (N), *s.n.* [Aug. 1886] (Al); *Engelmann s.n.* [St. Louis, Aug. 1843] (Pr), *s.n.* [St. Louis, 1861] (Br); *M. Martens s.n.* (Br).

xVERBENA DERMENI

This name was proposed by Moldenke (1946) for the hybrid produced

artificially between *V. hispida* Ruíz & Pav. and *V. bonariensis* L. and described by Dermen (1936). It has been found three times in the wild and I am certain that it occurs commonly where the ranges of the two species overlap, as in São Paulo, Brazil, in Paraguay, and in at least two provinces of Bolivia, two provinces of Chile, and nine provinces of Argentina. It seems very probable to me that some, at least, of the more or less "anomalous forms" of *V. brasiliensis* Vell. and of *V. litoralis* H.B.K. found in herbaria actually represent this hybrid, because its general habit is much like that of a slender-spiked *V. brasiliensis* or a dense-spiked *V. litoralis*. It is described as a suffrutescent herb 6-8 dm. tall, with lilac-blue flowers. Herbarium specimens of the hybrid have been identified as *V. bonariensis*, *V. litoralis*, and *V. bonariensis* var. *longibracteata* Kuntze. Bang found it at an altitude of 10,000 feet in the vicinity of La Paz, and Asplund at 3900 meters. Rojas collected it in flower and fruit in January, and Asplund found it in flower in April. It is referred to by Moldenke (1947a, 1949).

Material examined.—BOLIVIA. LA PAZ: *Asplund* 3565 (S, Us); *M. Bang* 204 (C). PARAGUAY: *T. Rojas* 2519 [Herb. Osten 18192] (F-photo, N, N-photo, Sg-photo, Ug-2 sheets, Z-photo).

xVERBENA DISSOLUTA

Moldenke (1955) proposed this name for the artificially produced hybrid between *V. laciniata* (L.) Briq. and *V. phlogiflora* Cham. described by Schnack and Covas (1945) as "*Glandularia laciniata* x *phlogiphlora*." The two parental species occur rather commonly in parts of Argentina, but I do not have any records of both from the same province in that country. In Uruguay, however, and in at least three states of Brazil they grow together, and natural examples of this hybrid may be expected there. It should, at all events, most certainly have considerable horticultural merit and so deserves further study and experimentation.

xVERBENA ENGELMANNII

One of the commonest of all natural hybrids in the genus *Verbena* is the one between *V. hastata* L. and *V. urticifolia* L., for which Moldenke (1937) proposed this name. It seems to occur abundantly where the ranges of these two species overlap in the eastern and central United States. That insects should so often transfer the pollen from one to the other of these two species is rather amazing, since, although they grow most commonly together, they are very different in general appearance — the one having very dense-flowered spikes of deep-blue flowers and the other very loose and lax distant-flowered spikes of white flowers. The hybrid resembles *V. urticifolia* in habit, but the spikes are denser, not greatly elongate after anthesis, very sparsely and irregularly fruited, the mature calyxes mostly contiguous, the corollas small and purplish, and the toothing of the leaves coarser and often double. The stems, branches, inflorescences, and leaves are subglabrous or sparsely strigillose.

Synonymous designations include the "*Verbena hastata* x *urticifolia*" of Blanchard, Dermen, Eggert, Farwell, Perry, and Pringle, the "*V. hastata* x

urticaefolia" of Blanchard, Chase, Dutton, McCoy, Norton, Pammel, and Peck, the "*V. urticaefolia* x *hastata*" of Farwell, the "*V. urticifolia* x *hastata*" of Gates and of Schneck, and the "*V. hybrida*" of Bicknell, as well as the *V. paniculato-urticaefolia* and *V. urticaefolio-paniculata* of Engelmann (1844). The "*V. hastata* x *urticifolia*" of Gates, however, is x*V. illicita,* at least insofar as the herbarium specimens which he annotated thus and which have been seen by me are concerned. The type collection of Bicknell's *V. hybrida* is his no. 7351, but the use of this binomial is pre-empted by the *V. hybrida* of Voss. The *Engelmann s.n.* [St. Louis, Aug. 1843], cited below, is regarded as the type collection of *V. paniculato-urticaefolia* Engelm., but my name is based on his *V. urticaefolio-paniculata,* of which the type collection is *Geyer s.n.* [Beardstown, July 1842].

The hybrid is referred to by Anon. (1915), Deam (1940), Deam *et al.* (1942, 1943, 1950), and Moldenke (1940, 1941, 1942a and b, 1947, 1949). It is described and illustrated by Gleason (1952).

Collectors have found it in low ground, creek bottoms, dooryards, swampy borders, marshy fields, cow pastures, and ditches, on moist or dry banks, sandy black oak dunes, and banks of field-draining ditches, along roadsides, in the vicinity of stockyards, and in low fields associated with *Teucrium canadense, Persicaria lapathifolia,* and *Carex vulpinoidea,* in flower and fruit from July to October and in December. The flowers are described by collectors as blue, violet-blue, "light-blue and caducous," pale lilac, purplish, or pale clear purple. Specimens in herbaria have been identified as either "parent," *V. carolina* L., *V. hastata* f. *rosea* Cheney, *V. officinalis* L., *V. riparia* Raf., *V. stricta* Vent., and *V. urticifolia* var. *riparia* Britton. As is to be expected, collectors' labels record the common names "blue vervain" and "nettle-leaved vervain."

Grimes considered his specimens, cited below, as a hybrid between "*V. urticaefolia*" and *V. stricta,* while Eggert identified some of his specimens as "*V. stricta* x *urticaefolia.*" Schneck found it growing among both "parents" in a dooryard and makes the comment that it looks like *V. urticifolia,* but the flowers are more like those of *V. hastata.* Shafer also says he found his specimens actually growing between both "parents." Deam describes his plants as being "almost as wide as tall," while Bicknell describes his as "long and spreading 2½ feet, surface of tube and throat within minutely puberulent, racemes flexuous, spreading and drooping, mostly 10 to 12 in. long, greatest spread of panicle 22 inches" and "rather more harshly hairy than *V. hastata,* leaves with more irregular and spreading teeth, flowers a little smaller and paler."

The *Grace* 353 cited below has very hirsute stems and does not look much like most specimens of the hybrid. Norton's no. 792 is a mixture with x*V. illicita.* Friesner's no. 6450 is very close to typical *V. hastata.* His nos. 18613, 18618, 18619, and 18620 were all growing together, he says. Of these, 18618 is typical *V. urticifolia,* 18613 is typical *V. hastata,* 18620 looks much like *V. hastata* and had "blue" flowers, while 18619 has more distant "pink" or "pinkish" flowers. The last-mentioned was regarded by him as F_2 material. Storm reports that his plants were "not numerous in about half acre of moist ground in stream bed." Gates records the hybrid from Crawford and Meade

counties, Kansas, while Deam and his associates report it from Fulton and Greene counties, Indiana.

Material examined.—VERMONT. ADDISON CO.: *Dutton s.n.* [Leicester, August 7, 1915] (Vt). BENNINGTON CO.: *W. H. Blanchard* 65 (N), *s.n.* [Aug. 11, 1902] Vt—2 sheets). CHITTENDEN CO.: *Pringle s.n.* [Charlotte, 15 July 1887] (Vt). WINDHAM CO.: *L. A. Wheeler s.n.* [Townshend, 8/23/23] (Go, S). NEW YORK. BRONX CO.: *E. P. Bicknell* 7336 (N), 7348 (N), 7350 (N), 7351 (N), 7352 (Al, It); *H. N. Moldenke* 18463 (Aa, Ec, Jr—2 sheets, Ml, N). NASSAU CO.: *E. P. Bicknell* 7353a (N), 7353e (N). TOMKINS CO.: *C. H. Peck s.n.* [Freeville] (Al). ULSTER CO.: *Elting* 2074 (Al). NEW JERSEY. MORRIS CO.: *Mackenzie* 4746 (N—2 sheets). PENNSYLVANIA. ALLEGHENY CO.: *Holz s.n.* [Pittsburgh, 1831] (S). CRAWFORD CO.: *Shafer s.n.* [July 23, 1901] (Cm). DELAWARE CO.: *F. W. Pennell* 14695 (Cm). MONTGOMERY CO.: *Wismer* 535 (Up). PHILADELPHIA CO.: *Bassett s.n.* [Pennypack Park, Oct. 5, 1927] (N). UNION CO.: *Westerfeld* 2377 (Ur). COUNTY UNDETERMINED: *Schweinitz s.n.* [1829] (Br). OHIO. LORAIN CO.: *A. A. Wright s.n.* [July 30, 1889] (Ob). LUCAS CO.: *Moseley s.n.* [Aug. 2, 1925] (Ob). ILLINOIS. ADAMS CO.: *R. A. Evers* 802, in part (Ur—2 sheets), 807 (Il). CASS CO.: *Geyer s.n.* [Beardstown, July 1842] (T—type). CHAMPAIGN CO.: *Ahles* 2911 (Ur—3 sheets). *R. A. Evers* 1604 (Ur); *G. N. Jones* 16761 (Ur). CRAWFORD CO.: *Ahles* 4900 (Ur—3 sheets). HARDIN CO.: *Ahles* 2754 (Ur). IROQUOIS CO.: *Ahles* 2538 (Ur); *Winterringer* 6452 (Il). JO DAVIESS CO.: *Pepoon & Moffatt* 254 (Ur). SANGAMON CO.: *G. D. Fuller* 5271 (Il), 5479 (Il), 6585 (Il). STEPHENSON CO.: *Eggert s.n.* [August 12, 1875] (I). TAZEWELL CO.: *V. H. Chase* 3230 (Al, Il, N, Ur). VERMILION CO.: *Storm s.n.* [July 28, 1949] (Ur). WABASH CO.: *Schneck s.n.* [Sept. 1, 1897] (Ur); *Schneck & Waite s.n.* [Herb. Univ. Ill. 30014] (Ur). WINNEBAGO CO.: *M. S. Bebb s.n.* [Fountaindale] (Al). INDIANA. BOONE CO.: *S. McCoy* 5294 (Bt). CARROLL CO.: *Ek s.n.* [west of Burlington, 8-7-1941] (Bt). CASS CO.: *Friesner* 6450 (Bt). CLINTON CO.: *C. C. Deam* 41978 (Dm). FRANKLIN CO.: *S. McCoy* 4170 (Dp). HANCOCK CO.: *Friesner* 18619 (Gg, N—2 sheets, Pl) 18620 (N—2 sheets); *S. McCoy* 828 (Dp). PUTNAM CO.: *Grimes* 2083 (Dp). WARRICK CO.: *C. C. Deam* 29006 (In). IOWA. CLAYTON CO.: *L. H. Pammel s.n.* [St. Olaf, Aug. 10, 1924] (Io). HARDIN CO.: *Peck s.n.* [Iowa Falls] (Io). JOHNSON CO.: *L. H. Pammel 708* (Io). LEE CO.: *I. Mitchell* 172 (Io). MUSCATINE CO.: *Pammel, Kelso & Harlan s.n.* [Jul. 20, 1919] (Io). POWESHIEK CO.: *M. E. Jones s.n.* [Grinnell, August 1875] (Po). STORY CO.: *J. R. Campbell* 67 (Io). TENNESSEE. CARROLL CO.: *Eggert s.n.* [Hollow Rock, 4 & 5 Aug. 1897] (Cm, N). MICHIGAN. CASS CO.: *Pepoon* 1347 (Mi). WAYNE CO.: *Farwell* 1426 (Fc), *s.n.* [Detroit, Sept. 25, 1893] (C); *H. H. Rusby s.n.* [Detroit, Aug. 1884] (Mi). WISCONSIN. DANE CO.: *C. C. Albers* 33015 (Au). KANSAS. BOURBON CO.: *Clothier & Whitford s.n.* [Aug. 11, 1897] (Ka). BROWN CO.: *F. Garner s.n.* [Summer, 1925] (Ka). CLOUD CO.: *Carleton s.n.* [July 18, 1888] (Ur). LINN CO.: *Brooks & Brooks s.n.* [1928] (Cm). NEMAHA CO.: *A. S. Hitchcock s.n.* [Dec. 11, 1896] (Ka). POTTAWATOMIE CO.: *Kimball s.n.* [St. George, Aug. 12, 1888] (Ka). REPUBLIC CO.: *F. A. Smith s.n.* [July 1896] (Ka). RILEY CO.: *J. B. Norton* 792, in part (Ka, N). MISSOURI. SAINT LOUIS CO.: *Eggert* 5323 (N), *s.n.* [Mississippi Valley, Aug. 4, 1873] (N), *s.n.* [St. Louis, Aug. 4, 1875] (Au, Cm—2 sheets, Du, Gg, Go, In, Io, Mn, N, Po, Up), *s.n.* [St. Louis, Aug. 8, 1875] (Au, Cm, Du, Gg, Io, Mn, N, Po, Up—2 sheets), *s.n.* [St. Louis, Aug. 1875] (Up), *s.n.* [12 Aug. 1877] (Al, I); *Engelmann s.n.* [St. Louis, Aug. 1843] (Br, Pr—2 sheets, T), *s.n.* [St. Louis] (Br, S, Sg); *Glatfelter s.n.* [near St. Louis, 8-10-94] (Mi); *M. Martens s.n.* (Br). OKLAHOMA. KINGFISHER CO.: *Grace* 353 (Ok). CULTIVATED. SPAIN: *Herb. Hort. Reg. Matrit.* 26 (Q). LOCALITY OF COLLECTION UNDESIGNATED: *A. Murray* 32 (S); *Swederus s.n.* (S).

xVERBENA FABRICATA

Dermen (1936) describes a hybrid which he produced artificially between *V. hispida* Ruiz & Pav. and *V. urticifolia* L. Moldenke (1955) proposed

the name x*V. fabricata* for this plant. The two "parent" species do not normally grow together anywhere, so it is not probable that the hybrid will ever be found in the wild. It is not likely to possess any horticultural merit, either.

xVerbena fecunda Moldenke, hybr. nov.

This binomial is hereby proposed for the fertile hybrids described by Dermen (1936) between *Verbena canadensis* (L.) Britton (including *V. canadensis* var. *atroviolacea* and *V. canadensis* var. *compacta*, and *V. ambrosifolia* var. *eglandulosa* Perry.

xVerbena ferax Moldenke, hybr. nov.

This binomial is hereby proposed for the fertile hybrids described by Dermen (1936) between *Verbena canadensis* (L.) Britton (including *V. canadensis* var. *atroviolacea* and *V. canadensis* var. *compacta*) and *V. racemosa* Eggert.

VERBENA HASTATA

MacDougal (1907) suggests that *Verbena hastata* L. may hybridize in the wild with *V. bracteosa* Michx. (now known as *V. bracteata* Lag. & Rodr.). However, he cites no specimens, gives no description, and does not say that he ever actually saw any such hybrid plants. I doubt very much whether the hybrid occurs.

xVERBENA HYBRIDA

This name was apparently first proposed for this commonly cultivated garden plant by Voss ex Rümpler (Vilmorin, 1879, 1894). Partial synonymy for this hybrid, as I regard it, is as follows: *Verbena buistii* Hort. (Harrison, 1840); *V. hendersonii* (Harrison, 1840); *V. melindres* var. *latifolia* Hort. (Bohn, 1844); *V. hybrida* var. *auriculata* Vilm. (Vilmorin, 1873); *V. hybrida* var. *striata* Vilm. (Vilmorin, 1873, 1888); *V. teucrioides* var. *auriculiflora* Regel (Regel, 1879); *V. hybrida* Hort. (Lindman, 1884); *V. hybrida* var. *grandiflora elegans* Regel (Regel, 1887); *V. hybrida* var. *auriculaeflora* Vilm. (Vilmorin, 1888); *V. hybrida* var. *atrocaerulea oculata* Vilm. (Vilmorin, 1894); *V. hybrida* var. *compacta* Hort. (Wittmark, 1902); *V. hortensis* Vilm. (Vilmorin, 1909); *V. hybrida* var. *compacta vesta* Hort. (H., 1911); *V. hybrida* var. *gigantea* Hort. (H., 1911); *V. hybrida* var. *alba* Hort. (Thompson and Morgan, 1930); *V. hybrida* var. *caerulea* Hort. (Thompson and Morgan, 1930); *V. hybrida* var. *colossea* Hort. (Thompson and Morgan, 1930); *V. hybrida* var. *rosea* Hort. (Thompson and Morgan, 1930); *V. hybrida* var. *purpurea* Hort. (Thompson and Morgan, 1930); *V. hybrida* var. *elegans* Hort. (Stapf, 1931); *V. hybrida* var. *nigro-violacea* Haage and Schmidt (Bailey, 1935); *V. hybrida* var. *lutea* Haage and Schmidt (Bailey, 1935); *V. hybrida* var. *candidissima* Haage and Schmidt (Bailey, 1935); *V. hybrida* var. *coccinea* Haage and Schmidt (Bailey, 1935); *V. grandiflora* Bodger (Harrow, 1936); *V. lutea* Waller-Franklin (Harrow, 1936); *V. luminosa* Waller-Franklin (Harrow, 1936); *V. rosea stellata* Bodger (Harrow, 1936);

V. coccinea Bodger (Harrow, 1936); *V. violacea stellata* Bodger (Harrow, 1936); *V. auricula* Park (Park, 1937); *V. striata* Park (Park, 1937); *V. colossea* Park (Park, 1937); *V. hortensis* Bailey (Moldenke, 1941); *V. hortensis* Hort. (Moldenke, 1941); *V. teucrioides* x *venosa* Hort. (Moldenke, 1941); *V. voglioni* Hort. (Moldenke, 1941); *V. hybrida* var. *grandiflora* Mitchell (Mitchell, 1944); *V. hibrida* Voss (Stellfeld, 1951).

It is an extremely polymorphic hybrid, and is planted for ornament practically throughout the civilized world. It often tends to escape from cultivation. The exact ancestry of the plant is not certain, but it is supposed to be a multiple hybrid of *V. platensis* Spreng., *V. phlogiflora* Cham., *V. incisa* Hook., and *V. peruviana* (L.) Britton, all of South America. The first-named "parent" is apparently the source of the white corollas seen in such varieties as *alba* and *candidissima* mentioned above and the fragrance characteristic of most varieties. The second-named "parent" apparently brings in the rosy and purple shades seen in vars. *caerulea, rosea, nigro-violacea,* and *purpurea.* The last two, namely *V. incisa* and *V. peruviana,* are probably the source of the red colors in var. *coccinea,* as well as the general leaf shape and procumbent habit of the plant.

Besides these Latin-named synonyms listed above, I regard the following horticultural and trade varieties as belonging to this hybrid: All-color Giant, American Beauty, Annapolis Blue, Apple Blossom, Beacon Light, Beauty of Oxford, Beauty of Oxford Hybrid, Blue Defiance, Blue Sentinel, Blue Shades, Brightness, Brilliant, Brilliant Giant, Burnett's Scarlet, Cameo Pink, Cardinal, Carmine Ball, Carmine Rose, Carter's Dwarf Coerulea, Carter's Dwarf Compact, Carter's Holborn Mammoth, Cerise Queen, Chamois, Coccinea, Coccinea Dwarfer, Crimson Glow, Crimson Seedling, Crown Prince, Danneborg, Dark Blue, Defiance, Defiance Re-selected, Dwarf Coerulea, Dwarf Compact, Elfin Scarlet, Elite, Ellen Willmott, Etna, Fairy Queen, Ferry, Fireball, Flame, Flamingo, Floradale Beauty, Fordhook Famous, Giant, Giant Auricula-flowered, Giant Erect Mixed, Giant Pink, Giant Salmon Pink, Gigantea, Golden Queen, Grandiflora Blue, Grandiflora White, Holborn Mammoth, Hybride Compacte Variée, Improved Mammoth, Johnson's Gigantea Mixed, Laurence Johnson, Lavender Glory, Lucifer, Lutea Improved, Magenta, Majestic Rose Shades, Mamath, Mammoth, Mammoth Mixed, Mammoth Pink, Mammoth Purple, Mammoth Rose Queen, Mammoth Scarlet, Mammoth Scarlet Queen, Mammoth Snow Queen, Mammoth White, Mayflower, Miss Millmott, New Giant Flowered, Newport Salmon, New Red, Oxford Pink, Pfitzer's Giant, Pink, Pink and Rose Shades, Pure White, Purple, Purple Garnet, Purple King, Purple Mantle, Red, Red Emperor, Rose, Rose Cardinal, Rosea Stellata, Roseglow, Rose Queen, Rose-red, Royal Blue, Royal Bouquet, Royale, Salmon Defiance, Salmon Pink, Salmon Queen, Scarlet, Scarlet Defiance, Scarlet Queen, Snow Queen, Snowball, Snowdrift, Snowstorm, Spectrum, Spectrum Red, Sutton's Giant Pink, Sutton's Giant Royal Blue, Violet Bouquet, White, White Beauty, and White-eye Blue Verbena.

Popular names for this plant are also numerous, including "alfombrilla," "aurikelblumige Verbenen," "barbînâ," "camaradinha," "common garden verbena," "common verbena," "corbeille fleurie," "estradeira," "Eisenkraut," "germanderblüssiga verbene," "germanderblüttiga verbena," "garten Eisenkraut," "güverein otu," "lipia," "shah's favourite," "sha-passan," "verbeina," "verbena," "verbêna," "verbena comune," "verbena de jardin," "verbena ibrida," "verveine," and "verveine commune." In herbaria specimens of this hybrid have been misidentified as *V. aubletia* Jacq., *V. chamaedryfolia* Juss., *V. drummondii* Baxt., *V. incisa* Hook., *V. lindleyi* Hort., *V. peruviana* (L.) Britton, *V. phlogiflora* Cham., *V. teneroides* Gill. & Hook., *V. teucrioides* Gill., and *V. venosa* Gill. & Hook.

The plants of this hybrid are often attacked by the fungus *Microsphaeria ferruginea* Erikss., according to Salmon (1900).

In addition to the references given above and in the synonymy of the

hybrid, descriptions and illustrations of it may also be found (Anon., 1846, 1879, 1880, 1884, 1950; Hulme and Hibberd, 1879-1887; Miller, 1891; Pynaert, 1903; Freeman and Williams, 1928; Guillaumin, 1930; Schaffner, 1933, 1934; Harrow, 1936; Bevedian, 1936; Grimm, 1937, 1938, 1943, 1947, 1948, 1952; Herter, 1937; Watkins, 1937; Goss, 1937; Crocker, 1938; Moldenke, 1939, 1939a, 1942, 1942a, 1944a and b, 1947, 1954; Barton, 1939; Scott-Moncrieff and Sturgess, 1940; Beale, 1940; Beale, Price, and Scott-Moncrieff, 1940; Questel, 1941; Calderón and Standley, 1941; MacMillan, 1943; Mitchell, 1944; Darlington and Janaki Ammal, 1945; Everett, 1945; Barton and Garman, 1946; Downer, 1947; Daniel, 1947; Stumpp and Walter, 1948, 1950; Burpee, 1949, 1952, 1953, 1954; Henderson, 1950; Kennedy, 1951; Stellfeld, 1951; Gleason, 1952; Henderson, Stumpp, and Walter, 1952, 1953; Garden, 1953; Johnson, 1953; Breck, 1954; Chandler, 1954, 1954a, b, c, d).

Material examined.—PENNSYLVANIA. BEAVER CO.: *Shafer s.n.* [Beaver Falls, Sept. 6, 1900] (Up). FLORIDA. BREVARD CO.: *J. K. Small* 8745 (N). IOWA. BOONE CO.: *Pammel & Pammel s.n.* [Ogden, Sept. 20, 1924] (Io). OKLAHOMA. PAYNE CO.: *Keeling* 64 (St). TEXAS. VAL VERDE CO.: *Parks & Cory* 9003 (Tr), 9004 (Tr). MEXICO. NUEVO LEON: *Roybal* 28 (W). COLOMBIA. ANTIOQUIA: *Toro Toro* 935 (Fn). BRAZIL. FEDERAL DISTRICT: *Frazão s.n.* [Herb. Jard. Bot. Rio de Jan. 7402] (N). MINAS GERAIS: *Sampaio* 21 [Herb. Rio de Jan. 46750] (Ja). SÃO PAULO: *Santoro s.n.* [Herb. Inst. Agron. S. Paulo 7613] (Be). SWEDEN. *Nilsson s.n.* [Sept. 1907] (Go); *Wide s.n.* [Malmö, Okt. 1897] (Go). BELGIAN CONGO. *Bredo* 1153 (Br). MADAGASCAR. *Baron 3619* (K, P); *Herb. Jard. Bot. Tananarive 1322* (P). CULTIVATED. VERMONT: *Dole* 346 (Vt); *Loveland s.n.* [Norwich, 3-22-92] (Vt). MASSACHUSETTS: *L. H. Bailey s.n.* [Cambridge, June 21-23, 1919] (Ba), *s.n.* [Cambridge, August 6-12, 1929] (Ba—2 sheets); *Carr s.n.* [Clinton] (Se); *A. Clark s.n.* [Amherst, July 1876] (Ms); *H. L. Jones s.n.* [Oct. 1893] (Ob); *Kidder s.n.* [7 Aug. 1929] (Oa); *Torrey & Cross s.n.* [Oct. 3, 1936] (Ms—2 sheets). CONNECTICUT: *Enequist* 152 (N). NEW YORK: *L. H. Bailey s.n.* [Sept. 1, 1915] (Ba), *s.n.* [Oct. 17, 1921] (Ba), *s.n.* [Sept. 4, 1922] (Ba), *s.n.* [Sept. 12, 1924] (Ba), *s.n.* [July 29, 1928] (Ba, Ba—2 photos, N—2 photos, Z—2 photos), *s.n.* [Aug. 5, 1928] (Ba), *s.n.* [Sept. 25, 1928] (Ba), *s.n.* [July 4, 1919] (Ba), *s.n.* [Aug. 13, 1924] (Ba), *s.n.* [Sept. 1, 1924] (Ba), *s.n.* [Sept. 20, 1925] (Ba), *s.n.* [July 22, 1926] (Ba—2 sheets), *s.n.* [July 25, 1926] (Ba), *s.n.* [Aug. 31, 1926] (Ba), *s.n.* [Sept. 8, 1926] (Ba), *s.n.* [Nov. 1, 1927] (Ba); *Burdick s.n.* [July 2, 1923] (Ba); *Collector undesignated s.n.* [Tarrytown, Aug. 1, '96] (N); *Jacobi s.n.* [N. Y. Bot. Gard. Cult. Pl. 26575; 6/15/10] (N), *s.n.* [N. Y. Bot. Gard. Cult. Pl. 26575; 7/8/10] (N), *s.n.* [N. Y. Bot. Gard. Cult. Pl. 26575; 8/1/10] (N); *Herb. N. Y. Bot. Gard. s.n.* [August 1, 1896] (N); *H. N. Moldenke* 8242 (N), 8243 (N), 8244 (N), 11887 (Cm, N), 11888 (Cm, N) 11893 (Cm, N), 11894 (Cm, N, St), 11895 (Cm, N, St), 11896 (Cm, N), 11897 (Cm, N, St), 11898 (Cm, N), 11899 (Cm, N), 11900 (Cm, N), 11901 (Cm, N); *N. Y. Bot. Gard. Cult. Pl.* 11100 (N—photo); *W. H. Rhoades s.n.* [near Rochester, July 1938] (Hs); *R. C. Schneider s.n.* [N. Y. Bot. Gard. Cult. Pl. 26575] (N); *A. Wood s.n.* (Pa). NEW JERSEY: *Disbrow s.n.* [Newark] (Nm); *H. N. Moldenke* 7858 (N). PENNSYLVANIA: *Burpee & Co. s.n.* [Doylestown] (Ba—2 sheets). DELAWARE: *Herb. Sullivant s.n.* (Pa). NORTH CAROLINA: *L. H. Bailey s.n.* [Washington, May 17, 1930] (Ba); *P. O. Schallert s.n.* [8/10/32] (Or). GEORGIA: *Cuthbert s.n.* [Augusta, June 1, 1900] (Fl). FLORIDA: *L. H. Bailey* 7022 (Ba); *Bailey & Bailey* 6468 (Ba), *s.n.* [Tallahassee, Apr. 3] (Ba—2 sheets); *G. B. Grant* 2503a (Po); *J. S. Watkins s.n.* [Gainesville, 3-20-31] (Fl). ALABAMA: *L. H. Bailey* 7048 (Ba). MISSISSIPPI: *L. H. Bailey* 7155 (Ba), 7156 (Ba). OHIO: *E. Wilkinson s.n.* [25 Sept. 1887] (Ob). ILLINOIS: *Herb. Div. Floric. Univ. Ill.* 176 (Ur), 273 (Ur), 886 (Ur); *Herb. Univ. Ill. s.n.* [Oct. 1, 1870] (Ur); *Stenstrom* 4 (Ur—2 sheets). IOWA: *Harmon s.n.* [Marshalltown, Oct. 7, 1929] (Io). NORTH DAKOTA: *Saint Lawrence* 494 (I). OKLAHOMA: *O. H.*

Calvert 220 (St); *Murphy* 99 (Ob). LOUISIANA: *Langlois s.n.* [August 1878] (I). TEXAS: *L. H. Bailey* 7398 (Ba); *C. L. Lundell* 10936 (N), 10939 (N), 10940 (Sm); *Lundell & Lundell* 9763 (Ld, N); *Reeves* 190 (N). OREGON: *G. M. Powell s.n.* [Aug. 8, 1933] (Or). CALIFORNIA: *Bailey & Bailey* 7960 (Ba), 9743 (Ba); *E. P. Bradbury s.n.* [Letts Hollywood, 1916] (Ba); *Eastwood s.n.* [Inverness, May 13, 1934] (Gg); *P. L. Hall* 63 (Ba); *Lenington s.n.* [Pomona, Dec. 15, 1927] (Hp), *s.n.* [Pomona, Feb. 16, 1928] (Hp); *Woodcock* 979 (Ba). MEXICO: *Collector undesignated* 1 (I), 59 (I); *M. B. Foster s.n.* (Ba); *Halbinger & Reko* 312 (N); *Moldenke & Moldenke* 19824 (N). PANAMA: *Maurice* 896 (W). BERMUDA: *Brown & Britton* 1728 (N); *Brown, Britton, & Bisset* 2209 (N). CUBA: *Fortun & Arias* 7066 (Es); *Herb. Est. Cent. Agron s.n.* [Nov. 1909] (Es); *Ponce & Ramos* 415 [Herb. Roig 317] (Rg); *Van Hermann* 867 (N), 2688 (N, Po). PUERTO RICO: *Moldenke & Moldenke* 19537 (N). ST. THOMAS: *Britton & Britton* 237 (N). BARBADOS: *Herb. Bot. Stat. Barbados* 322 (N). COLOMBIA: *Daniel* 2206 (W); *H. García y Barriga* 11619 (N); *Toro Toro* 1220 (Fn). VENEZUELA: *Bailey & Bailey* 884 (Ba), 1865 (Ba); *Elias* 158 (Oa). BRAZIL: *Etzel s.n.* [Herb. Inst. Bot. S. Paulo 38719] (Sp); *W. Hoehne* 2557 (Bh, N); *Moldenke & Moldenke* 19990 (N); *Stellfeld* 1095 [Herb. Mus. Parana. 1095] (N). URUGUAY: *Herb. Herter* 61714 (N); *Rosengurtt B.*3428 (N). ARGENTINA: *Burkart* 18105 (N); *Herb. Univ. Mass. s.n.* [Aug. 1864] (Ms); *T. Meyer* 12620 (N); *Moldenke & Moldenke* 19723 (N). FRANCE: *Herb. Harvey s.n.* [h.R.P. 1837] (Du); *Herb. Saldanha* 2769 (Ja). SWEDEN: *Bagge s.n.* [28/8/1910] (Go); *Herb. Beurling s.n.* [Holmiae, 1840] (S); *Lindström* 5 [1883] (Ew); *Reutermann s.n.* [31/7/1886] (Go), *s.n.* [13/9/1886] (Go); *Trolander* 5 (Ew); *E. Wall* 5 [18/841] (Ew—2 sheets), 5 [1/941] (Ew—2 sheets), 5 [15/941] (Ew). NETHERLANDS: *C. A. Backer s.n.* [Apeldoorn, 1915] (Bz). FINLAND: *Lindström* 5 [1903] (Ew). GERMANY: *Golenz s.n.* [Schwiebus, August 1872; Herb. Prager 18627] (Gg), *s.n.* [August] (Gg), *s.n.* [Schwiebus] (La); *Lohmeyer s.n.* (Du—2 sheets); *C. J. Mayer s.n.* [München, Sept. 1895] (Mi). AUSTRIA: *Khek s.n.* [Aug. '72] (V). SWITZERLAND: *Hort. Bot. Basil. s.n.* [Aug. 1841] (M). ITALY: *Herb. Harvey s.n.* [Hort. Bellorae, Jun. 1842] (Du). Madeira: *E. Wall* 5 [27/329] (Ew). BELGIAN CONGO: *RR.PP. Salèsiens* 291 (Br). INDIA: *Herb. Hort. Bot. Calcutt. s.n.* (Bz—2 sheets). CHINA: *Chiao* 12028 (Bz); *Lauphit* 113 (Ur); *Liu s.n.* [Peking Univ. Medical Coll.] (Ba). JAVA: *C. A. Backer* 12523 (Bz); *Herb. Hort. Bot. Bogor. XVK.A.XLIV.5* (Bz), *XVK.A.XLIV.9* (Bz), *XVK.A.XLV.3* (Bz), *XVK.A.XLV.12* (Bz), *XVK.A.XLV.13* (Bz), *XVK.A.XLV.20* (Bz), *XVK.A.XLVI.19* (Bz). LOCALITY UNDESIGNATED: *Collector undesignated s.n.* (Vt); *Herb. Mazziari* 1685 (S), 1687 (S), *s.n.* (S); *Herb. Univ. Mass. s.n.* [Oct. 1864] (Ms).

xVERBENA ILLICITA

This name was proposed by Moldenke (1937) for the natural hybrid between *V. stricta* Vent. and *V. urticifolia* L., which occurs commonly where the ranges of the two species overlap in the central United States. It is based on the *Verbena urticaefolio-stricta* of Engelmann (1844). Synonymous designations include "*Verbena stricta* x *urticaefolia*" of Mackenzie and of Pond, "*Verbena stricta* x *urticifolia*" of Britton, Bush, Eggert, Schneck, and Stevens (in part), "*Verbena urticifolia* x *stricta*" of Eggert and of Norton, and the *Verbena stricto-urticaefolia* of Engelmann (1844), of which Engelmann's unnumbered collection from St. Louis, July, 1842, is the type.

This hybrid is referred to by Gates (1940), Deam, Kriebel, Yuncker, and Friesner (1945), and Moldenke (1940, 1941, 1942a and b, 1947a, 1949). It is described and illustrated by Gleason (1952).

It resembles *V. urticifolia* in habit, but has the spikes denser, not greatly elongated after anthesis, very sparsely and irregularly fruited, the mature

calyxes mostly contiguous, the flowers larger, the leaves broader, and the stems, branches, inflorescences, and leaves densely and coarsely long-pubescent. The corollas are described as blue. Storm says it is "not numerous," growing among *V. stricta, V. hastata,* and *V. urticifolia.* Pammel reports it as "a common weed" (but probably refers to the true *V. urticifolia* with which he mixes it on herbarium sheets) associated with *V. stricta, V. hastata, Anthemis cotula, Persicaria mitis, Ambrosia elatior,* and *Coreopsis palmata.* Other collectors have found it in wet or sandy soil, pastures, meadows, and river-bottoms, at the edge of swamps, and along streets, flowering and fruiting from June through September. It has been identified in herbaria as one or the other "parent" and as *V. hastata* L., and has been called "blue vervain." Demaree found it at an elevation of 450 feet.

Material examined.—ILLINOIS. ALEXANDER CO.: *Eggert s.n.* [Cairo, Aug. 3, 1875] (Cm, Go, Io, N). CASS CO.: *Geyer s.n.* [July 1842] (Br). HANCOCK CO.: *L. H. Pammel s.n.* [Hamilton, Sept. 8, 1918] (Io). HENDERSON CO.: *H. N. Patterson s.n.* [July 1872] (Al). FULTON CO.: *Winterringer* 8834 (Il). MASON CO.: *Ahles* 2985 (Ur). MENARD CO.: *E. Hall s.n.* [Athens, 1861] (Pa). SANGAMON CO.: *Ahles* 4589 (Ur). VERMILION CO.: *Storm s.n.* [July 28, 1949] (Ur). WABASH CO.: *Schneck s.n.* [June 25, 1879] (Ur). WHITESIDE CO.: *Ahles* 4202 (Ur). CO. UNDETERMINED: *Eggert s.n.* [14 Aug. 1875] (I). INDIANA. TIPPECANOE CO.: *Dorner* 120 (Pu), 313 (Pu). IOWA. DES MOINES CO.: *L. H. Pammel* 960, in part (Io). HARDIN CO.: *McKibben s.n.* [Steam Boat Rock, Sept. 1912] (Io). WISCONSIN. WINNEBAGO CO.: *M. K. Clemens s.n.* [Oshkosh, July 30, 1909] (Po). KANSAS. DONIPHAN CO.: *Agrelius, Hall, Lovejoy, & Maroney s.n.* [8-18-13] (Lw). LABETTE CO.: *Clothier & Whitford s.n.* [Aug. 18, 1897] (Ka). POTTAWATOMIE CO.: *J. B. S. Norton s.n.* [7-17-96] (Ka); *R. H. Pond* 1130 (Ka, Mi, N). RILEY CO.: *J. B. S. Norton* 792, in part (Ka). WABAUNSEE CO.: *Norton & Clothier s.n.* [7-3-1895] (Ka). WYANDOTTE CO.: *Mackenzie s.n.* [June 27, 1895] (N). ARKANSAS. BAXTER CO.: *Demaree* 20686 (N). BENTON CO.: *E. N. Plank s.n.* (N). MISSOURI. COOPER CO.: *Bush* 12548 (Bt). FRANKLIN CO.: *Eggert s.n.* [Pacific, 4 July 1896] (Cm, N). MORGAN CO.: *Bush* 12927 (Ok). RALLS CO.: *J. Davis s.n.* [July 17, 1913] (Se). SAINT LOUIS CO.: *Eggert* 5319 (N), *s.n.* [14 Aug. 1875] (Al, Cm); *Engelmann s.n.* [St. Louis, Sept. 1841] (Pr—isotype), *s.n.* [St. Louis, July 1842] (Pr, T), *s.n.* [St. Louis, Aug. 1848] (T), *s.n.* (St. Louis, Aug. 1859] (T—2 sheets), *s.n.* [St. Louis] (Br, Sg). OKLAHOMA. OTTAWA CO.: *G. W. Stevens* 2308 (N).

xVERBENA INHONESTA

This name was proposed by Moldenke (1955) for the hybrid between *V. urticifolia* L. and *V. lasiostachys* Link produced artificially and described by Dermen (1936). These two species do not normally grow together in the wild, one "parent" being native to the eastern United States and the other west of the Rocky Mountains. It is probable, therefore, that this hybrid will never be found in the natural state unless the species become introduced in each other's territory.

xVERBENA INTERCEDENS

Briquet (1904) proposed this name for the natural hybrid between *V. bonariensis* L. and *V. ovata* Cham. It is referred to by Moldenke (1941b, 1942a and c, 1947a, 1949).

The hybrid is said to be "common" on the campo at Villarica. It grows to 1.1 meter tall and is said to have blue or violet corollas. It has been collected in anthesis and fruit in September, November, December, and January.

In herbaria it has been identified as *V. venosa* Gill. & Hook. and *V. bonariensis* var. *longibracteata* Kuntze. The Berro specimen cited below is very abnormal in appearance and may be virus-infected.

It is of interest to note that *V. ovata* — one of the reputed "parents" of this hybrid — has not yet been collected in Uruguay. One would suppose that both "parents" would be more plentiful than the hybrid and would, therefore, be collected sooner and more often. Yet there seems to be no doubt whatever that *V. ovata* is one of the ancestors of this hybrid.

Material examined.—PARAGUAY: *Hassler* 6149 [Macbride photos 17422] (Kr—photo of cotype, N—2 cotypes, N—photo of cotype, S—cotype), 8934 (V); *Jörgensen* 3770 [Herb. Osten 22245] (N, Ug), 3774 (N, S). URUGUAY: *Berro* 1626 (Ug); *Rosa-Mato* 728 [Herb. Mus. Hist. Nat. Montev. 10047] (Ug). ARGENTINA. MISIONES: *G. J. Schwartz* 1896 (N).

xVERBENA KONDAI

Moldenke (1946) proposed this name for the hybrid between *V. racemosa* Eggert and *V. tenuisecta* Briq., which was artificially produced and described by Dermen (1936) as "*V. racemosa* x *laciniata*." It is referred to by Moldenke (1947a, 1949). The two parental species grow in Texas, the former native and the latter introduced. As yet I have no record of them both from the same county, but *V. tenuisecta* is spreading very rapidly and it is only a matter of time before both will be growing in close proximity. The hybrid may then be expected in the wild. It ought to have considerable horticultural merit.

xVERBENA LECOCQI

This name was proposed by Moldenke (1946) for the hybrid produced artificially between *V. hispida* Ruiz & Pav. and what he called "*V. prostrata*" [actually *V. lasiostachys* Link] and which was described by Dermen (1936). These two species are not known to occur together in the wild state anywhere, so the hybrid is not to be expected in the wild. In view of the lack of attractiveness exhibited by both "parents," it is not likely to have any horticultural merit. It is referred to by Moldenke (1947a, 1949).

xVERBENA MATRITENSIS

This name was proposed by Moldenke (1947) for the natural or artificial hybrid between *V. carolina* L. and *V. hastata* L. It is known thus far only from a specimen in the botanic garden at Madrid, Spain, presumably in cultivation. It is listed by Salisbury (1953).

xVERBENA MERETRIX

Moldenke (1955) proposed this name for the artificially produced hybrid between *V. hispida* Ruiz & Pav. and *V. officinalis* L., described by Dermen (1936). The two species grow together in Cochabamba, Bolivia, and the hybrid may be expected there. They both also grow in Chile, but *V. officinalis* (a European species naturalized in Chile) is not yet known from the province where *V. hispida* is found. Both species, however, are weedy in character

and spread rapidly. It is probably only a matter of time before they also meet in that country. The hybrid probably has no horticultural merit.

xVERBENA MOECHINA

The natural hybrid between *V. simplex* Lehm. and *V. stricta* Vent. was given this name by Moldenke (1937), based on the *Verbena angustifolio-stricta* of Engelmann (1844). It occurs abundantly where the ranges of the two "parents" overlap in the central United States. It usually resembles *V. simplex* in habit, but has broader leaves, which are often elliptic or elliptic-ovate, more or less densely short-pubescent or velutinous beneath, the stems and branches usually densely pubescent, and the spikes poorly and irregularly fruited. From *V. stricta* it differs in its more slender and poorly-fruited spikes, smaller flowers, and narrower leaves.

The hybrid is referred to by Gates (1940), Kanda (1920), Deam (1940), Palmer (1916), Palmer and Steyermark (1935), and Moldenke (1940, 1941, 1942a and b, 1945a, 1947a, 1949). It is described and illustrated by Gleason (1952).

E. J. Palmer records the hybrid from Jasper Co., Missouri, but I have as yet not seen any substantiating specimens from that county. Collectors have found it on high ground along roadsides, open dry ground, sandy prairies, lime uplands, clay ridges, bluffs, and sand ridges, in rather sandy soil, pastures, and barrens, on sandy hills, along riversides, and in the vicinity of stockyards. Fell says it is "common in pastures," while Schopf found it "scattered over rolling open pastured hillsides." Deam's nos. 25586 and 26226 were actually collected in close association with *V. simplex*. It has been collected in anthesis and fruit from May through September, and at altitudes to 900 feet. Herbarium specimens have been identified as *V. angustifolia* Michx., *V. hastata* L., *V. spicata* Pammel, *V. stricta* var. *angustifolia* Martens, and *"Veronica angustifolia* Michx." Collectors' labels give the vernacular names "hoary verbena" and "la sacrée verveine."

Synonymous designations include the *"V. angustifolia* x *stricta"* of Bush, Eggert, Kellogg, and Rydberg, *"V. hastata* x *bracteosa"* of Pammel, *"V. simplex* x *stricta"* of Gates and of Hitchcock, *"V. stricta* x *angustifolia"* of Blankinship, Gates, Eggert (in part), Pammel, and Popenoe, *"V. stricta* x *urticaefolia"* of Letterman and of Pammel, and *Verbena stricto-angustifolia* of Engelmann (1844), of which the type collection is his unnumbered specimen from St. Louis, collected in July, 1842.

Material examined.—OHIO. ERIE CO.: *L. H. Pammel s.n.* [Sandusky, June & July, 1912] (Io). ILLINOIS. ADAMS CO.: *Evers* 1444 (Ur). PEORIA CO.: *F. E. McDonald s.n.* [Peoria, Jul. 1904] (Ur). POPE CO.: *Schopf* 6 (Il). SAINT CLAIR CO.: *Eggert s.n.* [12 Aug. 1875; Herb. Geete 5710] (Go, I). STEPHENSON CO.: *Eggert s.n.* [August 12, 1875] (I). WINNEBAGO CO.: *E. W. Fell* 51307 (Il), 51330 (Il), 51331 (Il). INDIANA. DAVIESS CO.: *C. C. Deam* 25586 (In). HARRISON CO.: *C. C. Deam* 20357 (N—type, Pu—isotype), 20357a (Dm). MARION CO.: *C. C. Deam* 6953 (Dm). ORANGE CO.: *C. C. Deam* 26226 (Dm). WASHINGTON CO.: *C. C. Deam* 20603 (Dm). IOWA. BLACK HAWK CO.: *Burk* 594 (Ur); *L. H. Pammel s.n.* [Cedar Falls, Sept. 28, 1920] (Io); *Pammel, Fisk, & Gilbert* 272 (N). CERRO GORDO CO.: *Hayden* 1, in part (N—9 sheets), 3, in part (N—10 sheets). HARDIN CO.: *L. H. Pammel s.n.* [Steam

Boat Rock, 9-1912] (Io). JONES CO.: *L. H. Pammel s.n.* [Oxford Junction, Jul. 25, 1919] (Io—2 sheets). O'BRIEN CO.: *Winge s.n.* [Calumet, May 1911] (Cp). STORY CO.: *C. R. Ball s.n.* [June 30, 1898] (Io); *L. H. Pammel s.n.* [Ames, 9-8-94] (Io). KENTUCKY. WARREN CO.: *S. F. Price s.n.* [Bowling Green] (N). KANSAS. GREENWOOD CO.: *W. H. Horr s.n.* [July 28, 1930] (Lw). LEAVENWORTH CO.: *Jahns s.n.* [June 27, 1929] (Lw). MIAMI CO.: *Oyster s.n.* [Aug. 1885; Herb. Prager 18624] (Gg). MONTGOMERY CO.: *A. S. Hitchcock s.n.* [Aug. 1896] (Ka); *Rydberg & Imler* 434 (Ka, Lw, N). SHAWNEE CO.: *A. S. Hitchcock s.n.* [July 1896] (Ka); *E. A. Popenoe s.n.* [Topeka, July 7, 1879] (Ka). MISSOURI. BARRY CO.: *Bush 15613* (Ka). FRANKLIN CO.: *Eggert s.n.* [Pacific, 4 July 1896] (Au, Cm, Io, Mn); *L. H. Pammel s.n.* [Washington, 6/25/88] (Io). GREENE CO.: *Blankinship s.n.* [July 17, 1919] (Po). JACKSON CO.: *C. A. Ripley s.n.* [July 1898] (Ob). JEFFERSON CO.: *H. N. Andrews Jr. s.n.* [Herculaneum, 5/30/36] (Ms) PHELPS CO.: *Kellogg s.n.* [Jerome, June 20, 1912] (N). PIKE CO.: *J. Davis* 3379 (Ur). POLK CO.: *Steyermark* 24049 (Ky). SAINT LOUIS CO.: *Eggert s.n.* [12 Aug. 1875] (Al, N); *Engelmann s.n.* [St. Louis, July 1842] (Pr, T), *s.n.* [St. Louis] (Br); *Letterman s.n.* [Allenton, June 1884] (Io), *s.n.* [Allenton, June 28, 1911] (Au, Io, N); *M. Martens s.n.* (Br—2 sheets). STONE CO.: *Bush* 15697 (Ka), *s.n.* [Oct. 9, 1936] (Md). ARKANSAS. BAXTER CO.: *Demaree* 29320 (N). FULTON CO.: *Demaree* 26322 (N). LAWRENCE CO.: *Rolfs s.n.* [8/91] (Io). NEWTON CO.: *Demaree* 22244a (N). PULASKI CO.: *Hasse s.n.* [Little Rock, May 30] (N). CULTIVATED. BELGIUM: *M. Martens s.n.* [h.b.L.] (Br).

VERBENA NEOMEXICANA

Briquet (1894) mentions, without description, a "*Verbena neo-mexicana*" which he says is a hybrid between *V. canescens* H.B.K. and *V. officinalis* L. I have no doubt that he was referring to the plant which we now call *V. neomexicana* (A. Gray) Small, growing abundantly in Texas, New Mexico and adjacent parts of Arizona and Mexico. I do not believe that it is of hybrid origin; certainly one of the two putative parents, *V. officinalis*, is found only very seldom as an introduction in that area.

xVERBENA NEQUAM

This name was proposed by Moldenke (1955) for the hybrid between *V. laciniata* (L.) Briq. and *V. dissecta* Willd., produced artificially and described by Schnack and Covas (1945) as "*Glandularia laciniata* x *dissecta*." These two specimens occur together in at least two states of Brazil, in Uruguay, and in at least six provinces of Argentina. It is possible that they occur together also in parts of Bolivia and Chile. One might expect to find the hybrid in the wild where the ranges of the parent species overlap. It is very possible that some of the almost innumerable "forms" or "variants" now generally regarded as *V. laciniata, V. dissecta, V. tenuisecta, V. santiaguensis, V. mendocina,* or other species in this complex may actually represent this hybrid. The hybrid should certainly have considerable horticultural merit.

xVERBENA NOACKI

Moldenke proposed this name for the hybrid between *V. hispida* Ruíz & Pav. and *V. hastata* L. produced artificially and described by Dermen (1936). These two species do not normally grow together in the wild — one being temperate South American and the other temperate North American. It is not expected that this hybrid, therefore, will ever be found in the wild.

It might, however, have horticultural possibilities. It is referred to by Moldenke (1947a, 1949).

xVERBENA OKLAHOMENSIS

This name was proposed by Moldenke (1942a) for what appears to be a natural hybrid between *V. canadensis* (L.) Britton and *V. bipinnatifida* Nutt. These two species grow together in at least nine counties of Kansas, two of Arkansas, eleven of Oklahoma, nineteen of Texas, one county each of Missouri and Nebraska, and two parishes of Louisiana, so it is very possible that the hybrid will be found more often. It may even account for some of the tremendous "variability" noted in herbarium material now usually regarded as one or the other of its "parents." The Pitts collection cited below is a mixture of the hybrid with *V. bipinnatifida*, while the Van Vleet specimen consists of a mixture with *V. canadensis*, indicating, apparently, the very close proximity of at least one of the "parents" in each case. The Demaree specimen was originally identified as *V. ciliata* var. *longidentata* Perry, and was collected on sandy hills, flowering and fruiting in April. The hybrid is referred to by Moldenke (1947a, 1949). It should have considerable horticultural merit.

Material examined.—OKLAHOMA. CLEVELAND CO.: *Pitts s.n.* [4/19/15] (Ok—type, Ok—isotype). COMANCHE CO.: *Van Vleet s.n.* [Mt. Sheridan, 7/4/03] (Ok). TILLMAN CO.: *Demaree* 12188 (Ok).

xVERBENA OSTENI

This name was proposed by Moldenke (1947) for the natural hybrid between *V. peruviana* (L.) Britton and *V. platensis* Spreng. which apparently occurs sporadically where the ranges of the two parent species overlap in Uruguay. It is listed by Salisbury (1953).

Material examined.—URUGUAY: *Castellanos s.n.* [Herb. Inst. Miguel Lillo 15048] (N); *Herter* 1000 [Herb. Herter 82763] (Ca, N), 1000a [Herb. Herter 83913] (Ca, N); *Legrand* 3491 (Ug); *Osten* 3177, in part (N, Ug).

xVERBENA PERRIANA

Moldenke (1937) proposed this name for the natural hybrid between *V. bracteata* Lag. & Rodr. and *V. urticifolia* L., found rather commonly where the ranges of these two species overlap in central North America and based on the *Verbena urticaefolio-bracteosa* of Engelmann (1844), of which cotypes were collected by Geyer at Beardstown and by Engelmann in St. Louis in July, 1842. It resembles *V. braceata* in habit, but is stouter, more erect, with broad and laciniate rather than dissected leaves, long and slender spikes, and smaller bractlets which usually only slightly surpass the calyx, are usually not conspicuous nor foliaceous, and are mostly only 3-4 mm long.

Synonymous designations include the "*Verbena bracteosa* x *hastata*" of Mackenzie, Rydberg (1917, 1932) and Webber (1892), "*V. bracteosa* x *stricta*" of Britton, Clothier, Palmer, and Schnack, "*V. bracteosa* x *urticaefolia*" of Carleton, Deam, and Mackenzie, "*V. bracteosa* x *urticifolia*" of Eggert,

Rydberg (1932), and Stevens, "*V. hastata* x *bracteosa*" of Rydberg and of Schneck, "*V. officinalis* x *bracteosa*" of Barnes, "*V. stricta* x *bracteosa*" of Hitchcock, "*V. stricta* x *urticifolia*" of Stevens (in part), "*V. urticifolia* x *bracteosa*" of Eggert, "*V. bracteoso-urticaefolia*" of Engelmann (1844) and "*V. bracteoso-stricta*" and "*V. stricto-bracteosa*" of the same collector. The hybrid is referred to also by Palmer (1916), Wolden (1932), Gates (1940), Deam (1940, 1946), and Moldenke (1940, 1941, 1942a and b, 1945a, 1947, 1949). It is described and illustrated by Gleason (1952).

Collectors have found this hybrid in very sandy soil, clayey soil, dry ground, waste places, barnyards, sandy open ground, woods and grassy woods, and bottomlands, along roadsides, and on or near river banks, blooming and fruiting from June through August. Its flowers are said to be blue. Schneck reports that it blooms when *V. hastata* is not yet in flower and that "the flowers when fresh are very much like [those of *V.*] *hastata* in shape and color [but the] whole plant [is] procumbent." A specimen in the Columbia University Herbarium with no collector designated, bears the note "Erect or half prostrate. . . . I find it assuming the erect position while young only. My best specimens are from those which are half prostrate. This species is plentiful here. Brendel thinks it is only one of the many hybrids." Dodge says it is "plentiful" at Point Edwards, Ontario. Schacklette reports it as "a weed of meadows and pastures" in Kentucky. Deam describes it as a large diffuse plant or sprawling, with assurgent stems and many diffuse branches. Besides the records represented by the specimens cited below, Gates reports it from McPherson County, Kansas. Herbarium specimens have been mis-identified as either of its two "parents," *V. canadensis* (L.) Britton, *V. officinalis* L., and even *V. spuria* L. W. H. Rhoades records the names "pigeon grass," "holy-herb," "enchanter's plant," "European vervain," and "Juno's-tears" for this plant, but these are names applied to *V. officinalis* with which he mis-identified his collection.

Material examined.—ONTARIO. LAMBTON CO.: *C. K. Dodge s.n.* [Point Edward, July 27, 1902] (Mi—3 sheets). ILLINOIS. ADAMS CO.: *Seymour s.n.* [Fall Creek, July 29, 1879] (Ur). CASS CO.: *Geyer s.n.* [Beardstown, July 1842] (Pr—cotype, T—2 cotypes). FULTON CO.: *L. Wolf s.n.* [Canton, 1874] (Al). HANCOCK CO.: *S. B. Mead s.n.* [Augusta, 1842] (Pr), *s.n.* [Augusta, June 1844] (C). HENDERSON CO.: *H. N. Patterson s.n.* [July] (Al). MENARD CO.: *E. Hall s.n.* [Athens, Aug. 1866] (Ms). MONROE CO.: *Winterringer* 3814 (Il). WABASH CO.: *Schneck s.n.* [June 25, 1879] (Ur), *s.n.* [July 8, 1880] (Ur), *s.n.* [Mt. Carmel, June 15/88] (Ur). INDIANA. FULTON CO.: *C. C. Deam* 39228 (Al, Dm). JENNINGS CO.: *C. R. Barnes* 28 (N). JOHNSON CO.: *W. H. Rhoades s.n.* [Edinberg] (Hs). KOSCIUSKO CO.: *C. C. Deam* 55323 (Dm). LAGRANGE CO.: *C. C. Deam* 36661 (Dm). LAWRENCE CO.: *C. C. Deam* 17287 (Dm). IOWA. BLACK HAWK CO.: *Carver s.n.* [Cedar Falls, July 5, 1895] (Io). CLARKE CO.: *Pammel & Pammel s.n.* [Osceola, Sept. 27, 1924] (Io). DECATUR CO.: *J. P. Anderson s.n.* [July 23, 1903] (Io). EMMET CO.: *Wolden s.n.* [Estherville, Aug. 5, 1922] (Io), *s.n.* [Estherville, Jul. 12, 1927] (Io). FREMONT CO.: *A. S. Hitchcock s.n.* [Hamburg] (Io, Ka). HARDIN CO.: *M. E. Jones s.n.* [Iowa Falls, Aug. 1876] (Po). JOHNSON CO.: *A. S. Hitchcock s.n.* [Iowa City] (Io). STORY CO.: *Carver s.n.* [Ames, July 14, 1896] (Io); *L. Leonard s.n.* [Collins, Aug. 8, 1929] (Io). KENTUCKY. UNION CO.: Shacklette 499 (Ky). COUNTY UNDETERMINED: *Short s.n.* [barrens of Ky., 1840] (Pr). WISCONSIN. LA CROSSE CO.: *L. H. Pammel s.n.* [La Crosse, 7-20-1887] (Io). LAFAYETTE CO.: *Manning s.n.* [Shulesburg, July 19, 1883] (N). MILWAUKEE CO.: *J. S. Douglas s.n.* [Wis.] (Je). KANSAS. POTTAWATOMIE CO.:

Clothier s.n. [St. George, 7-4-96] (Ka); *A. S. Hitchcock* 972 (Ka, N). SEDGWICK CO.: *Carleton* 276 (Du). MISSOURI. JACKSON CO.: *Mackenzie s.n.* [July 19, 1896] (N), *s.n.* [Little Blue Tank, Aug. 2, 1896] (N, Ur). JASPER CO.: *E. J. Palmer* 4025 (Ur). SAINT LOUIS CO.: *Eggert* 5318 (N), *s.n.* [4 Aug. 1875] (Cm), *s.n.* [near Eureka, July 28, 1879] (Al, Cm, Vt), *s.n.* [Glencoe, 28 July 1879] (Cm, N); *Engelmann s.n.* [St. Louis, July 1842] (Br—cotype, F—photo of cotype, N—photo of cotype, Pr—cotype, S—2 cotypes, Si—photo of cotype, T—cotype, Z—photo of cotype), *s.n.* [St. Louis, Aug. 1859] (Br, T), *s.n.* [Aug. 1843] (T), *s.n.* [Amer. bor.] (Br, S, Sg). ARKANSAS. BENTON CO.: *Plank s.n.* (N). NEBRASKA. SAUNDERS CO.: *Rydberg* 153 (N), *s.n.* [Mead, June 1890] (C). OKLAHOMA. WOODS CO.: *G. W. Stevens* 1703 (Du, N, St, Ur). WASHINGTON. KLICKITAT CO.: *Suksdorf s.n.* [July 9, 1898] (N). LOCALITY OF COLLECTION UNDESIGNATED: *Collector undesignated* 27 (C), 103 (Q).

VERBENA PINNATIFIDA

Briquet (1894) refers to *Verbena pinnatifida* Lam. as a hybrid between *V. hastata* L. and *V. officinalis* L. I believe that this was merely a guess on his part because of the more or less hastately lobed condition of the leaves, which Lamarck inaccurately described as "pinnatifid," on the plant in question. Actually, Lamarck's plant is only a form of the very common eastern North American *V. hastata*, and I do not think that it is of hybrid origin. Certainly the European *V. officinalis* very seldom grows in close proximity to *V. hastata*.

xVERBENA PROSTIBULA

This name was proposed by Moldenke (1955) for the hybrid between *V. hispida* Ruiz & Pav. and *V. simplex* Lehm., produced artificially and described by Dermen (1936). Since these two species do not grow together in the wild anywhere, as far as I am aware, there is little chance of ever finding this hybrid in nature. Both species, however, occur in cultivation — especially in Europe — and the hybrid might have horticultural possibilities.

xVERBENA RYDBERGII

Moldenke (1937) proposed this name for the natural hybrid between *V. hastata* L. and *V. stricta* Vent. which occurs commonly where the ranges of these two species overlap in the central United States. It is based on the *Verbena paniculato-stricta* of Engelmann (1844), of which the type was collected by Engelmann on the banks of the Mississippi River at St. Louis in July, 1843. Synonymous designations include the "*V. bracteosa* x *stricta*" of Deam, Eggert, and Rydberg (1917, 1932), "*V. hastata* x *stricta*" of Anderson, Gates, and Rydberg (1894, 1895), "*V. paniculata* x *stricta*" of Engelmann (Anderson, Gates, and Rydberg, 1895), "*V. stricta* x *hastata*" of Eggert, Gates (in part), Hill, Kellerman, Patterson, and Schneck, "*V. stricta* x *urticaefolia*" of Eggert, "*V. stricta* x *urticifolia*" of Glatfelter, Patterson, and Stevens (in part), "*V. stricto-hastata*" of Patterson, and "*V. stricto-paniculata*" of Engelmann (1844), of which the type was collected by him at St. Louis in July, 1842. The "*V. hastata* x *stricta*" of Elmore, however, appears to be typical *V. hastata*, and that of Allen is *V. stricta* f. *albiflora* Wadmond. The "*V. stricta* x *hastata*" of Allen is typical *V. stricta*.

The hybrid is referred to by Gates (1940), Kanda (1920), Deam, *et al.*

(1945, 1948) and Moldenke (1940, 1941, 1942a and b, 1947a, 1949). It is described and illustrated by Gleason (1952). In addition to the records represented by the specimens cited below, Gates records it from Cloud, Osborne, and Shawnee counties, Kansas. Kanda gives a cytological discussion of it and says that Dr. Chamberlain is authority for the statement that Hugo De Vries looked at specimens and stated definitely that they were not mutants, but hybrids instead. He says they are "often albino." Herbarium specimens are often identified as either "parent" or even as *V. officinalis*.

x*V. rydbergii* resembles *V. hastata* in habit, but its leaves are more reticulate-venose, densely velutinous beneath, the corolla is larger, the bractlets are ovate-lanceolate, about 4 mm long, and not carinate, and the calyx is 4-5 mm long. Fruit is produced sparingly. The flowers are said to be bright bluish-purple, lilac-blue, or pink. It has been collected in anthesis and fruit from June through August, in low marshy land, waste ground, moist soil, sandy fields, pastures, open woods, wet ground of streambeds, marshy areas around ponds, and wet or sandy soil in general, on badly eroded hillsides, along low grassy roadsides, and at the junction of moist and dry bottoms. The Pammel collections from Lyon County, Iowa, and Hancock County, Illinois, are actually mixtures with *V. stricta*, indicating the close proximity of at least that one "parent" species. Ahles reports that he found the hybrid growing in association with both "parents" and with *V. urticifolia*.

Material examined.—ILLINOIS. BUREAU CO.: *Ahles* 4176 (Ur); *Winterringer* 8008 (Il). CHAMPAIGN CO.: *G. N. Jones* 12525 (Ur). COOK CO.: *E. J. Hill* 160.1898 (Ur—3 sheets); *L. N. Johnson s.n.* [Herb. Univ. Ill. 17462] (Ur). DE KALB CO.: *P. B. Whitford* 156 (Il). FULTON CO.: *Winterringer* 8864 (Il). HANCOCK CO.: *L. H. Pammel s.n.* [Hamilton, Sept. 8, 1918] (Io). HENDERSON CO.: *H. N. Patterson s.n.* [August 1872] (Al), *s.n.* [Oquawka, July] (Io—2 sheets). LA SALLE CO.: *Thone* 87 (Ur). PIKE CO.: *J. Davis* 3241 (Ur), *s.n.* [July 18, 1914] (Se). SANGAMON CO.: *G. D. Fuller* 6406 (Il); *J. C. McGregor* 11174 (Il). VERMILION CO.: *Storm s.n.* [July 28, 1949] (Ur—2 sheets). WABASH CO.: *Schneck s.n.* [Mt. Carmel, Sept. 1, 1887] (Ur), *s.n.* [June 1900] (Ur). WINNEBAGO CO.: *E. W. Fell* 51324 (Il), 51328 (Il), 51329 (Il), 51404 (Il). INDIANA. PULASKI CO.: *Friesner* 22372 (N). WASHINGTON CO.: *C. C. Deam* 20603 (N—2 sheets, Pu). IOWA. CHEROKEE CO.: *L. H. Pammel s.n.* [Cherokee, Oct. 17, '24] (Io). CLAY CO.: *Hayden* 3003 (Io), 3006 (Io, N). DALLAS CO.: *L. H. Pammel s.n.* [Dawson, Aug. 16, 1918] (Io). DECATUR CO.: *J. P. Anderson s.n.* [Aug. 25, 1904] (Io). HANCOCK CO.: *L. H. Pammel s.n.* [Garner, Jul. 27, 1918] (Io); *Pammel & MacDonald s.n.* [Goodell, Jul. 12, 1922] (Io). HARDIN CO.: *L. H. Pammel s.n.* [Steamboat Rocks, 9-12-12] (Io—2 sheets), *s.n.* [Eldora, Oct. 5, 1924] (Io). LYON CO.: *L. H. Pammel s.n.* [Granite, Sept. 1, 1920] (Io). PALO ALTO CO.: *L. H. Pammel s.n.* [Jul. 18, 1920] (Io). POWESHIEK CO.: *Conard s.n.* [8-29-1927] (Ok); *M. E. Jones s.n.* [Grinnell, Aug. 1877] (Du). STORY CO.: *L. H. Pammel s.n.* [Ames, 1902] (Io). WINNESHIEK CO.: *Tolstead s.n.* [Decorah, July 23, 1934] (Io). WISCONSIN. GRANT CO.: *L. H. Pammel s.n.* [Muscoda, Aug. 1928] (Io). TREMPEALEAU CO.: *L. H. Pammel s.n.* [Trempealeau, 7-20-82] (Io). MINNESOTA. HENNEPIN CO.: *Sandberg 605* (Ka). KANSAS. ATCHISON CO.: *A. S. Hitchcock s.n.* [Oct. 1896] (Ka). BARBER CO.: *Horr & Franklin s.n.* [July 6, 1940] (Lw). BROWN CO.: *Clothier & Whitford s.n.* [July 29, 1897] (Ka). CHAUTAUQUA CO.: *W. H. Horr s.n.* [July 6, 1930] (Lw). CHEROKEE CO.: *Kellerman s.n.* [Galena, July 8, 1887] (Ka). ELK CO.: *Clothier & Whitford s.n.* [Aug. 20 & 21, 1897] (Ka). ELLIS CO.: *E. Runyon* 280 (Dm). JEFFERSON CO.: *Harman* 40 (Ka). JEWELL CO.: *J. B. S. Norton s.n.* [Webber, Sept. 23, 1895] (Ka). LEAVENWORTH CO.: *W. H. Horr s.n.* [6/14/30] (Lw). MARSHALL CO.: *A. S. Hitchcock s.n.* [Dec. 10, 1896] (Ka). NEMAHA CO.: *A. S. Hitchcock s.n.* [Dec. 11, 1896] (Ka). POTTAWATOMIE CO.:

Clothier s.n. [St. George, Aug. 28, 1896] (Ka). COUNTY UNDETERMINED: *Kleeberger s.n.* (Gg). MISSOURI. SAINT LOUIS CO.: *Eggert* 5320 (N), *s.n.* [4 Aug. 1875] (C, Go, Po), *s.n.* [St. Louis, Aug. 1875] (Au, Ba, Cm, Du, Gg, Io, Mn, N, Po), *s.n.* [12 Aug. 1877] (Al), *s.n.* [19 Aug. 1877] (Cm, I); *Englemann s.n.* [July 1839] (Br), *s.n.* [St. Louis, July 1842] (Pr, T), *s.n.* [banks of Mississippi, July 1843] (T—type), *s.n.* [St. Louis] (S); *Glatfelter s.n.* [near St. Louis, 8-11-94] (Mi); *Lejeune s.n.* (Br); *Letterman s.n.* [Allenton, June 28, 1911] (N). ARKANSAS. BENTON CO.: *Heacox s.n.* [July 20, '89] (Ob). NEBRASKA. BANNER CO.: *Rydberg 1564* (N—2 sheets). CEDAR CO.: *Clements* 2663½ (C). THOMAS CO.: *Krautter s.n.* [Halsey, July 23, 1907] (Up—4 sheets). OKLAHOMA. GRANT CO.: *G. W. Stevens* 1791 (Ur). MIAMI CO.: *G. W. Stevens A.*2308 (St). OTTAWA CO.: *Schendel* 202 (St); *G. W. Stevens* 2308, in part (Du, N, Ok). LOCALITY OF COLLECTION UNDESIGNATED: *Short s.n.* ["banks of the Wabash"] (Pr).

xVERBENA SCHNACKII

This name was proposed by Moldenke (1946) for the hybrid which was artificially produced by Schnack and Covas (1945) between *V. peruviana* (L.) Britton and *V. megapotamica* Spreng., but which they published as "*Glandularia peruviana* x *megapotamica*." The two species grow together in at least two states of Brazil, in Paraguay and Uruguay, and in at least one province of Argentina, so it is possible that the hybrid may be found in the wild. In fact some of the "anomalous" specimens distributed as one species or the other in herbaria may represent this hybrid. It should certainly have considerable horticultural merit, as both "parents" are handsome-flowered.

xVERBENA SCORTA

Moldenke (1955) proposed this name for the artificially produced hybrid between *V. halei* Small and *V. lasiostachys* Link, which was described by Dermen (1936). These two species do not grow together actually, as far as I am aware, anywhere, so it is not very probable that the hybrid will ever be found in the wild, unless one species or the other eventually invades the territory now occupied by the other in the southwestern part of the United States.

VERBENA SIMPLEX

MacDougal (1907) suggests that *V. angustifolia* Michx. (now called *V. simplex* Lehm.) may hybridize in the wild with *V. bracteosa* Michx. (now known as *V. bracteata* Lag. & Rodr.). However, he cites no examples, gives no description and does not actually say that he ever saw such hybrid plants. I doubt very much whether the hybrid occurs.

xVERBENA SUKSDORFI

This name was proposed by Moldenke (1946) for the natural or artificial hybrid between *V. officinalis* L. and *V. lasiostachys* var. *septentrionalis* Moldenke, found by Suksdorf in a garden at Bingen, Washington, in 1904. The same hybrid has been produced artificially by Dermen and is referred to by him as *Verbena officinalis* x *prostrata*. The source of Suksdorf's plant is not known, and neither of the parents is known to occur in the state of

Washington. The type and only specimen which I have seen is deposited in the Herbarium of the State College of Washington at Pullman.

xVERBENA TEASH

Moldenke (1941a) proposed this name for the artificially produced hybrid between x*V. hybrida* Voss and *V. tenuisecta* Briq., first produced in the nurseries of Edward Teas at Houston, Texas, and called "*V. hybrida* x *erinoides*" by him, but typified by a collection made by G. A. Stevens (no. 4) at Harrisburg, Pennsylvania, and collected on June 20, 1933. Under this name, x*V. teasii*, I include the garden varieties called Albion, Bellaire, Ceres, Madge Roberts, Rowena, Ruth, and Teas Hybrid Verbenas. The corollas are white (Albion), pink (Rowena, Ruth), purplish (Bellaire), or dark red (Ceres). It has been collected in anthesis in April, June, July, and October, so apparently has a long blooming period. It is referred to by Moldenke (1941, 1942b, 1944b, 1947a, 1949). It was misidentified as *V. incisa* Hook. by Ekman.

Material examined.—CULTIVATED. NEW YORK: *L. H. Bailey s.n.* [July 27, 1927] (Ba—4 sheets), *s.n.* [Oct. 3, 1927] (Ba). PENNSYLVANIA: *G. A. Stevens* 1 (Ba), 2 (Ba), 3 (Ba), 4 (Ba—type, N—photo of type, Z—photo of type). TEXAS: *L. H. Bailey* 7394 (Ba), 7395 (Ba), 7396 (Ba); *Teas s.n.* [June 2, 1926] (Ba), *s.n.* [June 1926] (Ba—5 sheets). CALIFORNIA: *Bailey & Bailey* 9830 (Ba). HAITI: *Ekman* H.9357 (S).

xVERBENA TORPA

Moldenke (1955) proposed this name for the hybrid between *V. urticifolia* L. and *V. neomexicana* (A. Gray) Small, produced artificially and described by Dermen (1936). The two "parents" do not grow together naturally anywhere, as far as I am aware, although both occur in Texas and a variety of *V. neomexicana* has been found as a waif in Baltimore, Maryland, where *V. urticifolia* is common. It is not very probable that this hybrid will be found in the wild unless the two parental species invade each other's territory in the future.

xVERBENA TRANSITORIA

This name was proposed by Moldenke (1955) for the hybrid produced artificially between *V. laciniata* (L.) Briq. and *V. megapotamica* Spreng., and described by Covas and Schnack (1945) as "*Glandularia laciniata* x *megapotamica*." The two species grow together in Uruguay and in the state of Rio Grande do Sul, Brazil, and so it is possible that this hybrid may be found in the wild state in these areas. They also both grow in Argentina, but, as far as I know now, not in the same province. The hybrid should have considerable horticultural merit and deserves further experimentation.

xVERBENA VAGA

Moldenke (1955a) proposed this name for the hybrid between *V. santiaguensis* (Covas & Schnack) Moldenke and *V. megapotamica* Spreng., produced artificially and described by Covas and Schnack (1945) as "*Glandularia*

santiaguensis x *megapotamica*." The two parental species grow together in Uruguay and the hybrid may be expected in the wild state there. They both also grow in parts of Argentina, but, as far as I know, not in the same provinces. The hybrid should offer considerable horticultural promise and deserves more experimental work.

xVERBENA WINGEI

This name was proposed by Moldenke (1944) for the artificially produced hybrid between *V. tenuisecta* Briq. and *V. canadensis* (L.) Britton described by Winge (1938) as "*Verbena tenera* x *aubletia*." The two species are often grown together in gardens and are found wild in at least two parishes of Louisiana, twelve counties of Texas, and one county each in Alabama and Florida. *V. tenuisecta* is spreading rapidly in our southern states. Already it is wild in five counties of Alabama, four of Mississippi, sixteen of Florida, twenty-eight of Georgia, and sixteen of Texas. *V. canadensis* is native in all these states, so the hybrid is to be expected throughout that area. It is referred to by Moldenke (1947a, 1949).

xVERONICENA HAARTMANI

Moldenke (1955) proposed this name for the plant described, illustrated, and called *xVeronica hybrida* (Haartman, 1751) and *xVeronica spuria* (Haartman, 1756). Neither specific epithet which he used is available for the hybrid because the former is regarded as pre-Linnean and the other is invalidated by the *Veronica spuria* of Linneus (1753). Haartman considered his plant to be a hybrid between *Veronica maritima* L. and *Verbena officinalis* L.

The status of this plant is highly questionable and it is hoped that by thus calling attention to it more information about it and its antecedents may become available. Its existence seems to have been rather generally ignored by, or unknown to, later workers. I have not as yet seen the type — if, indeed, any such was ever preserved — but among the 146,000 herbarium specimens that have passed through my hands in the past 27 years there were two specimens which may possibly have represented that same or a similar taxon. Unfortunately, not being aware myself of Haartman's paper at the time these reached me, I returned them to their respective institutional owners with the simple annotation "Not verbenaceous!" and kept no record of them. My recollection of them, however, is that they represented a plant much like the one figured by Haartman. The sheets on which they were mounted — as I recall them now — were both quite old and had apparently been bandied about from one genus and family to another, always to be returned to the herbarium owning them with the comment that they did not belong in that group. I recall "Scroph.?," "Labiat.?," and even "Lobeliac.?" inscribed on at least one of them, with each suggestion later stricken out by pencil. Perhaps the curators of the herbaria in question, on reading this, may recall the specimens and may re-examine them again in the light of Haartman's claims. Unfortunately, having studied material of my groups from 242 herbaria, I cannot now recall in which herbaria they are deposited.

As far as I am aware, this claim of Haartman is the first for a hybrid between species belonging to entirely different families of either plants or animals. If any readers know of any other such claims I would appreciate learning of them. Generally such an inter-family hybrid is regarded as biologically impossible, and this alone tends to cast much doubt on Haartman's claim. Of course, in the modern classification of the flowering plants by J. Hutchinson the *Scrophulariaceae*, in which family *Veronica* belongs, is regarded as the direct ancestor of the *Verbenaceae*. The morphological characters of *Veronica* and *Verbena* are very similar in many respects — especially in respect to the two species supposed to be involved here — but are quite different in others. Both groups are composed of annual or perennial herbs (with some shrubby or even arborescent species included by "lumpers") with opposite (or alternate, rarely whorled) leaves which are exstipulate and with mostly small blue, purple, pink, or white, complete, and irregular flowers borne in axillary or terminal racemes or spicate inflorescences, or solitary. The calyx is gamosepalous, inferior, campanulate or tubular, and persistent in both, 4- or 5-toothed in *Verbena* or -cleft in *Veronica*. The corolla in both is gamopetalous, but is mostly rotate and with a very short tube in *Veronica* and mostly infundibular or hypocrateriform with a long slender tube in *Verbena*. The corolla-limb in both is deeply and more or less unequally 4- or 5-lobed (mostly 4-lobed in *Veronica*, mostly 5-lobed in *Verbena*) and somewhat 2-lipped. In *Verbena* there are normally four fertile and didynamous stamens, inserted in the corolla-tube, and alternate with the corolla-lobes, but some species included in the genus by "lumpers" have the fertile stamens reduced to two. In *Veronica* there are always only two fertile stamens, divergent, and inserted at either side and at the base of the upper corolla-lobe. In *Veronica* the two anthers are obtuse, their two thecae confluent at the summit. In *Verbena* the anthers are very similar, but the sacs are usually not confluent and the connective is in some species (perhaps better segregated as the genus *Glandularia*) appendaged. In both genera there are slender filaments and there is a single, superior, compound, 2-carpellary pistil. In *Verbena* the ovary is 4-celled (or less by abortion), with one ovule in each cavity; in *Veronica* it is only 2-celled, with "few" to numerous ovules in each cell. In both groups the ovules are anatropous or amphitropous. In *Verbena* the style is usually short and 2-lobed at the summit, only one of the lobes being stigmatiferous. In *Veronica* the style is slender and the single stigma is capitate. The fruit in *Verbena* is a dry schizocarp, mostly enclosed by the calyx, at length usually separating into four 1-seeded, linear or linear-oblong, crustaceous, smooth, papillose, or rugose nutlets or cocci. In *Veronica* the fruit is a more or less compressed capsule, sometimes very flat, emarginate, obcordate, or 2-lobed, and loculicidally dehiscent, containing seeds that are smooth or rough, flat, plano-convex, or excavated on the inner face.

In *Veronica* the haploid number of chromosomes is 7, 8, 9, 10, or 21. In the true genus *Verbena* [or its section *Verbenaca*, if *Glandularia* is included in *Verbena*] the number is 7. *Verbena officinalis* has a chromosome formula of $x = 7$; the formula in *Veronica maritima* is $x_2 = 17$ $(8 + 9)$ according to Darlington & Janaki Ammal (1945). It is hoped that cytologists will

examine this question and see if Haartman's plant can be produced by the hybridization which he suggests.

"xVITEX ADULTERINA"

This name appears first in Hill (1926) and was then copied by Moldenke (1942a, 1949). Hill credits the name to Haussknecht (1897), but in this reference Haussknecht is proposing the name *Verbena adulterina* for the natural hybrid between *V. officinalis* and *V. supina*. Through some clerical error in filing and alphabetizing, Hill placed the specific epithet under the genus *Vitex* instead of *Verbena*. There is no such plant as "x*Vitex adulterina*."

VITEX BREVILABIATA

Ducke (1932) suggests that *Herb. Rio de Janerio* 22529 represents a natural hybrid between *Vitex triflora* Vahl and *V. orinocensis* H. B. K. and that therefore his *V. brevilabiata* Ducke is the same hybrid. The collection referred to, however, is certainly *V. klugii* Moldenke and is not at all identical with the collections cited by him as *V. brevilabiata*. I regard both taxa as valid species and not as hybrids.

"xVITEX HYBRIDA"

This name was proposed by Moldenke (1941) for what then was supposed to be a natural hybrid between *V. agnus-castus* L. and *V. negundo* L. It was based on an unnumbered specimen collected by Bhole in Sind, Pakistan, in July, 1891. I now feel that this specimen represents what is currently called *V. agnus-castus* var. *pseudo-negundo* (Hausskn.) Bornm. The characters of this variety are, indeed, more or less intermediate between *V. agnus-castus* and *V. negundo*, but it appears to grow mostly where one supposed "parent" does not occur. *V. agnus-castus* is a typically Mediterranean plant, found wild from Portugal and Spain through southern France, Italy, Corsica, Sardinia, Sicily, the Balearic, Ionian, and Aegean Islands, Cyprus, Crete, Malta, Yugoslavia, and Greece, north to southern Germany and Hungary, east to Transcaucasia, Turkomen, and Sind, and south through Turkey, Syria, Iraq, Lebanon, and Israel to Morocco and Algeria. It has been introduced and naturalized in Natal, the southeastern United States, and elsewhere.

V. negundo, on the other hand, is found from the Northwestern Provinces of Pakistan, India, and Ceylon, through parts of China, Japan, Formosa, Hongkong, Hainan, the Lantau Islands, Annam Cambodia, Malacca, and Penang, to the Philippines, Java, Sarawak, the Lesser Sunda Islands, and Guam; also in Mauritius and Madagascar, but probably introduced.

The so-called variety *pseudo-negundo* is known from Turkomen and Turkey through Syria and Israel and east to Iran, Afghanistan, Baluchistan, and Sind. It is apparent, therefore, that it does not occur naturally anywhere with both supposed "parents" although usually with one or the other. Eig, Feinbrun, and Zohary (printed notes on distributed herbarium specimen, collection no. 280) are of the opinion that it is a

. . . sub-Irano-Turanian plant, penetrating into the Mediterranean region. We are somewhat in doubt about the specific value of the plant, which is closely related to *V. agnus-castus*, although it presents very distinct differential characters, such as a bearded lower lip and smaller corollas. Although the area of this species and that of *V. agnus-castus* partly overlap, we consider *V. pseudo-negundo* an Irano-Turanian plant, penetrating into the Mediterranean region, whereas *V. agnus-castus* is a plant of the Mediterranean element penetrating into the Irano-Turanian region. In Palestine we found *V. pseudo-negundo* from the Shelfela and from different places in the Jordan Valley (both Upper and Lower). *V. agnus-castus* was found by us in the Sharon, in the Judean mountains, and in the Upper Galilee. The habitat of *V. pseudo-negundo* is banks of watercourses, where it is a principal plant of the Viticetum pseudo-negundi. We have encountered this association (or one approaching it in composition), with *V. pseudo-negundo* as the principal species, along rivers and wadies in Iraquian Kurdistan.

H. J. Lam (1919) suggests that *Volkens* 425 from the island of Yap may be a hybrid between *Vitex negundo* var. *bicolor* H. J. Lam and *V. trifolia* L. I have examined this collection and in my opinion it represents typical *Vitex trifolia* var. *bicolor* (Willd.) Moldenke and is not of hybrid origin but represents a very common and widespread taxon which is best awarded a varietal status.

All things considered, therefore, "x*Vitex hybrida*" is probably not a hybrid.

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Vascular Plants of Pontotoc County, Oklahoma[1]

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After making observations and periodic collections of the flora of Pontotoc County for several years, the author felt that a more intensive study should be made. He therefore chose to make the taxonomic study of the vascular plants indigenous to, or naturalized in, the county. Collections were made during the years 1948 through 1952, but most collecting was done in 1951 and 1952.

Intensive collections were made at a number of stations that had distinctly different ecological conditions so that as many different species as possible could be found. These areas were visited at intervals of about two weeks during the growing season. At the same time a constant search was being made for other sites of still different ecological conditions so that new areas could be added.

Specimens were prepared, pressed, and identified by the author. They are deposited in the herbarium of the Oklahoma State University (formerly the Oklahoma Agricultural and Mechanical College). In addition to the collections made by the author, some plants that are listed were collected by others and are found in the Bebb Herbarium of the University of Oklahoma. The latter material was examined carefully and in some instances reidentified by the author. These are designated by citation of collector and collection number followed by the symbol "OU."

In accordance with the latest revision of the International Rules of Botanical Nomenclature (Rickett, 1951) the typical variety is designated by a repetition of the specific epithet without author citation, in instances where more than one variety of a species has been described. This is illustrated with the following example: *Oenothera missouriensis* Sims, var. *missouriensis* becomes the name of the typical variety, since other taxons differing from this, but considered of varietal rank, have been described, such as *Oenothera missouriensis* Sims, var. *oklahomensis* (Norton) Munz.

Acknowledgment.—This work was carried on at the Oklahoma State University, where the library and herbarium were at the writer's disposal. For these privileges and many others, the author wishes to express his appreciation. He is especially grateful to Professor U. T. Waterfall, under whose supervision the study was made. His constant encouragement and helpful guidance were of invaluable assistance throughout the course of the investigations, as well as in the preparation of this paper. The very helpful suggestions made by the author's advisory committee during the preparation of this paper are also greatly appreciated. He also wishes to express his appreciation and thanks to Dr. G. J. Goodman, Curator of the Bebb Herbarium of the University of Oklahoma, Norman, for the loan of collections from that herbarium.

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PHYSICAL FEATURES

LOCATION AND SIZE

Pontotoc County is in south-central Oklahoma. Its northern boundary is the South Canadian River. It extends from township one north to township six north, inclusive, and from range four east to range eight east inclusive. It is within the great physiographic province of Central United States known as the Central Lowland, and in the section of Oklahoma which is often referred to as the "Cross Timbers."

The county contains seventeen whole townships and parts of six others. The total area is 717 square miles, with a total of 458,880 acres.

TOPOGRAPHY

Pontotoc County consists of rolling to gently rolling prairies, forested steep slopes, and some very rough, hilly terrain. An escarpment extends from the southeast corner of the county to a point near the southwest limits of the city of Ada. It consists of a strip of broken land, about 3 miles in width, that divides the southeast portion into two distinct high plains. The higher plain, south of the escarpment and stretching across the entire southern portion of the county, has comparatively smooth relief. The stony hilltops and broad shallow valleys are covered by a rich soil of decomposed limestone and shale. (Fitzpatrick and Goke, 1941: Nos. 1-5). This plain lies at an elevation of 1100 to 1300 ft. above sea level, and is well drained by tributaries of the Blue River. It slopes gently to the southeast and contains dolomitic limestone on the eastern margin. Farther west it is underlain with sandstone.

The plain north of the escarpment, and extending across the entire northern portion of the county, is strongly rolling and in some sections is deeply cut. In general, the valleys are deeper than those of the southern plain, and in many places angular slopes appear as a result of solid sandstone outcrops. This plain has an elevation of 800 to 1100 ft. The northern portion of this area is drained northward and eastward by tributaries of the South Canadian River. In the southeast portion of this plain the drainage is eastward and southeastward into Muddy Boggy Creek and Clear Boggy Creek. Sandstone is dominant on this plain, but some shale, granitic conglomerate, limestone, and old river deposits of sandy clay are also present.

GEOLOGY

The exposed strata of the county range in age from upper Cambrian to Recent (Conkling, 1927). In the northern part, Pennsylvanian Sandstone and Pennsylvanian Shale prevail, while a smaller area of the south contains outcroppings of Arbuckle Limestone of the Ordovician and Cambrian periods. Fringing the latter are smaller areas of Viola Limestone and Simpson Formation.*

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* Geological map of Oklahoma. Compiled by Hugh D. Miser of the U. S. Geol. Surv., 1923 and 1924.

History

One of the earliest plant collections from this area was made by C. S. Sheldon during the months of June, July, and August, 1891 (Holzinger, 1892). This collection was made during a tour through this area under the auspices of the U. S. Dept. of Agriculture. The plants were stored in the U. S. National Herbarium, Washington, D. C. He listed a total of 21 species collected in the vicinity of Stonewall, Chickasaw Nation, in what is now Pontotoc County. These included five grasses, four composites and three legumes, with each of nine other families represented by only one species. He was assisted by L. H. Bailey, who verified identifications of the carices, and George Vasey, who determined the grasses.

During the years 1934 through 1941 Churchill W. Thomas, Professor of Botany at East Central Oklahoma State College, Ada, collected many plants from various sections of the county. He established the East Central Herbarium, in which these plants were placed and where some of them remain.

G. Thomas Robbins, who served as professor of botany at the same college during the years 1946 through 1948, continued collections of the county flora. Some of his duplicates were distributed among various herbaria, including the Bebb Herbarium of the University of Oklahoma and the Tracy Herbarium of the Texas Agricultural and Mechanical College, as well as the herbaria of the Southern Methodist University, the University of California, and the New York Botanical Garden. Among his collections were *Phacelia hirsuta* from Pontotoc County (Constance, 1949).

Climate

The climate of Pontotoc County is distinctly continental (Yearbook of Agriculture, 1941; Weather Bureau, 1949). High summer temperatures almost invariably occur with clear skies, and are attended by dry, or moderately dry, winds from south or southwest. Occasionally, hot winds accompany the high temperatures and cause rapid evaporation of moisture. When these conditions persist for considerable periods, severe droughts often follow. Clear skies and dry atmosphere facilitate rapid radiation, therefore the summer nights are usually cool. In general, the winters are comparatively mild and of short duration. Over a period of 30 years, the average temperature for January was 40.4°F and that for July was 82.9°F. In the same period there was a maximum of 116°F and a minimum of –10°F. During the years 1949—1952, the average temperatures for January and July departed only slightly from that of the longer period. In this four year period the maximum and minimum were 108°F and 0°F respectively.

Rains occur more often, and are more general, during the spring and early summer, while they are more local and uncertain for the remainder of the year. According to records kept in Ada for a period of 32 years, the average total annual precipitation is 37.82 inches. The months April, May, and June have the highest averages with 3.81 in., 5.49 in., and 4.31 in. respectively. The months of January, February, and December show the lowest amount of precipitation with 2.19 in., 1.75 in., and 2.13 in. respectively.

Snowfall produces a portion of this, but is so infrequent as to be of minor importance.

During the years 1949, 1950, 1951, and 1952, in which most collections were made, considerable variation from the average precipitation occurred. In 1949 the total precipitation was 17.7 percent above average and in 1950 it was 24.5 percent above average. However, during the next two years in which the most intensive collecting was done, there was a very marked decrease in total precipitation. In 1951 the total precipitation measured only 27.92 in., which was 26.6 percent below the 32 year average. The year 1952 had a measurement of only 26.87 in., or 29.3 percent below the 32 year average.

The average date of the latest killing frost, as determined for a 30 year period is March 26, and the latest on record is April 25. The average date of the earliest killing frost is November 6, and the earliest on record is October 19. The average frost-free period is 226 days, a comparatively long growing period.

The prevailing wind direction in the county is southerly, although in December, January, and February northerly winds predominate. The average wind velocity is low.

The average annual number of clear days is 195, partly cloudy days 90, and cloudy days 80. Sunshine is abundant, averaging 66 percent of the total possible time.

ECOLOGY

GENERAL FEATURES

Pontotoc County lies within a wide belt extending across Oklahoma in a north-south direction, which is characterized by the presence of only a portion of the eastern hardwood forest and an increase in prairie vegetation. The transitional nature of this belt may be observed in the vegetation of the county, since the dominant vegetation of the eastern portion is oak-hickory forest and that of the western portion is sub-climax tall-grass prairie.

Approximately 60 percent of the total area has never been disturbed by cultivation. Of this area, almost one-half is composed of rough stony lands that are unsuited for the growth of cultivated crops (Fitzpatrick and Goke, 1941: No. 4). A second large portion has productive soils, but has been utilized for pasture, now being occupied mostly by large ranches. A third non-cultivated area of much less extent is that of low flood plains, largely along the South Canadian River, where overflows often occur.

The portions of the county that have been cultivated are widely scattered and are divided between those of high ridges or slopes, and those of flood plains. In either case they are mostly confined to the soils of sandstone and shale origin, since those of limestone areas are stony and rough.

ROUGH STONY LANDS

The rough stony lands are not restricted to a designated portion of the county, but are much more common in the eastern and northeastern sections. In this area there are many cliffs and steep slopes, between which often occur small spring-fed streams. The surface soil is a very shallow layer of sandy

or gravelly loam which is readily eroded when exposed. The most prominent association here is oak-hickory forest, with *Quercus stellata*, and *Q. marilandica* as the dominants (Weaver and Clements, 1938). Greater numbers of the latter grow as small scrubby trees on dry sandy exposed hillsides while the former make up an increasingly greater portion of the timber, where the habitat conditions are more favorable. Constantly associated with these, on the lower slopes, and along the ravines are *Carya tomentosa*, *C. cordiformis*, *C. texana*, *Quercus Muhlenbergii*, *Q. Shumardii* var. *Schneckii*, and *Ulmus americana*. Characteristic thickets of open areas are *Rhus glabra*, *with* occasional, more local thickets of *R. copallina* var. *latifolia* and *Symphoricarpos orbiculatus*.

Prevernal species are not numerous in the oak-hickory forest, but usually include *Antennaria plantaginifolia* and *Galium Aparine* on shaded slopes. In less sheltered situations of the hillsides, *Nothoscordum bivalve*, *Physalis heterophylla* var. *heterophylla* and *Viola Kitaibeliana* var. *Rafinesquii* are early flowering plants. In moist soils of the stream banks are such plants as *Senecio obovatus* var. *rotundus*, *Erigeron philadelphicus* and *Viola missouriensis*.

Some of the more common vernal species of the shaded slopes are *Scutellaria parvula* var. *australis*, *Triodanis perfoliata*, *Achillea lanulosa*, *Erigeron tenuis* and *Oxalis violacea* var. *violacea*. In less sheltered areas of the hillsides the most prominent vernal plants include *Tephrosia virginiana*, *Oxalis stricta*, *Triodanis biflorus*, *Rhus glabra*, *R. copallina* var. *latifolia*, *R. aromatica* var. *serotina*, *Erythronium albidum* var. *mesochorum*, *Desmanthus leptolobus* and *Daucus pusillus*. On the lower slopes and stream margins, such plants as *Sanicula canadensis*, *Geum canadense* var. *camporum*, *Lippia nodiflora*, *L. lanceolata* var. *recognita*, *Veronica peregrina* var. *xalapensis*, *Pyrrhopappus Geiseri* and *Cornus florida* are commonly seen.

Prominent among the estival species of the high woodland hillsides are such low perennial herbs as *Agrimonia pubescens*, *Acalypha virginica*, *A. gracilens* var. *monococca* and *Mollugo verticillata*, as well as the low woody species, *Ampelopsis arborea*, *Berchemia scandens* and *Ceanothus americanus*. Common in the more open areas of this seasonal aspect are *Sabatia angularis*, *S. campestris*, *Amsonia ciliata*, *Asclepias tuberosa*, *A. viridis*, *Phacelia hirsuta*, *Gilia rubra*, *Verbena simplex*, *V. canadensis*, *Crotalaria sagittalis* and *Dalea purpurea*. The areas of greater soil moisture are characterized in the openings by the low herbaceous climbing vines, *Clitoria mariana* and *Galactia volubilis* var. *mississippiensis*, and in the scattered woods by the somewhat taller *Strophostyles helvola* and *Tephrosia virginiana*. The estival vegetation that flourishes on the forest floor along the hillside ravines and brooks consists of such species as *Bidens bipinnata*, *Heliopsis helianthoides* var. *scabra*, *Tragia urticifolia*, *Parietaria pensylvanica* and the climbing vines, *Parthenocissus quinquefolia*, *Vitis cinerea*, *V. Lincecumii* var. *glauca*, *V. vulpina*, *Cocculus carolinus* and *Menispermum canadense*. Also very common in this habitat are *Smilax Bonanox*, *S. glauca* var. *leurophylla* and *S. tamnoides*, which may be climbers if their tendrils reach the larger plants, but often exist as dense low thickets.

Serotinal species of the woodland hilltops and slopes in the oak-hickory association include the grasses, *Panicum lanuginosum* var. *fasciculatum*, *P.*

sphaerocarpon, P. oligosanthes, and, in the more xeric habitats, *Eragrostis pilosa* and *Aristida adscensionis.* Associated with these are the sedges *Carex Muhlenbergii* var. *Muhlenbergii, C. retroflexa* and *C. Bicknellii.* Other common herbaceous species are *Erigeron tenuis, Eupatorium serotinum* and *Solidago ulmifolia.* Some of these shade-tolerant, fall-flowering species may also be found in the open woods of the same sandy or gravelly hillsides. Other more prominent plants of this habitat are *Aster exilis, Lespedeza stipulacea, L. Stuevei* var. *Stuevei, Vernonia Baldwini* var. *interior, Andropogon scoparius, A. ternarius, Bouteloua hirsuta* var. *hirsuta* and *Rubus trivialis.* Along the margins of the rocky streams this seasonal aspect contains *Elephantopus carolinianus, Helenium tenuifolium, Rumex crispus, R. altissimus, Polygonum pensylvanicum* var. *laevigatum, Panicum anceps* and *Triodia flava.*

Another large section of the rough stony lands occurs in an unbroken belt several miles in width which extends from a point near Ada to the southeast corner of the county. The northeast half of this belt is deeply cut by transverse ravines, across which there is a drop of about two hundred to three hundred feet in a distance of two to four miles. In general the vegetation is very similar to that of the previously described area of broken lands in the northeastern portion of the county.

The southwest half of the same belt is a high escarpment of limestones and shales with a very thin layer of surface soil, and in most places is so thickly covered with rocks as to support only scanty vegetation. The outcropping rocks are of Arbuckle Limestone. The few trees that grow here are only scrubby forms of *Celtis laevigata, Viburnum rufidulum, Ulmus alata* and *Crataegus mollis.* Subclimax tall-grass prairie predominates in this region, and the dominants are *Andropogon scoparius, Bouteloua hirsuta* and *B. curtipendula,* with many thickets of *Rhus aromatica* var. *serotina* showing prominence in some areas.

The common prevernal species of this habitat are *Hedyotis minima, Viola Kitaibeliana* var. *Rafinesquii, Nothoscordum bivalve, Androstephium coeruleum, Astranthium integrifolium, Chaetopappa asteroides, Draba reptans, D. brachycarpa, D. cuneifolia, Descurainia pinnata* var. *brachycarpa, Capsella bursa-pastoris* and *Carex blanda.*

The more common vernal species are *Dodecatheon Meadia* var. *Meadia, Oxalis stricta, O. violacea* var. *violacea, Sisyrinchium angustifolium, Yucca glauca,* var. *glauca, Nemastylis geminiflora, Allium canadense* var. *mobilense, A. Drummondii, Sonchus asper, Bifora americana, Baptisia leucophaea, Verbena bipinnatifida, Androsace occidentalis,* and *Carex austrina.* Replacing some of these in the latter part of May are *Sedum pulchellum* and *Valerianella amarella,* which are often very abundant in large communities.

During the months of June, July, and August the true vernal species are replaced almost completely by the flowering of the following species of the estival aspect: *Vicia hirsuta, Hedeoma Drummondii, Lomatium foeniculaceum, Heliotropium tenellum, Dalea purpureum, D. aurea, Triodanis leptocarpa, Hypericum sphaerocarpum, Opuntia humifusa, Centaurea americana, Cirsium altissimum* and *Thelespermum intermedium.*

The serotinal aspect is likely to contain such grasses as *Andropogon sac-*

charoides, A. ternarius, Aristida oligantha and *Eragrostis oxylepis* var. *oxylepis*, along with the following dominants of this rough area: *Andropogon scoparius, Bouteloua curtipendula* and *Bouteloua hirsuta*. Also this high rocky limestone plain often contains *Solidago altissima, S. rigida, Aster ericoides* and *Cassia fasciculata*.

PRAIRIES

South and southwest of the escarpment which extends from near Ada to the southeast corner of the county, there is a high limestone prairie with many outcroppings. Only a very small portion of this prairie has ever been disturbed by cultivation of crops, due partially to its rocky nature and partially to its value as pasture land. The few exceptions are the farming areas sometimes found along Blue River, which has its headwaters in this area.

There are many smaller areas in the western part of the county, extending from the city of Roff northward and northwestward to a line extending from Ada northwestward to the boundary line, some four miles south of the South Canadian River. These prairies contain soils that are derived principally from sandstones, shales, and conglomerates. The vegetation is so similar to that of the limestone prairies of the south as to permit their being described together.

Throughout these subclimax tall-grass prairies the Andropogon-Bouteloua faciation predominates, with *Andropogon scoparius, Bouteloua curtipendula* and *B. hirsuta* as the dominants, and in the shallow valleys of deeper and richer soil there is often a good growth of *Andropogon Gerardi*.

Very few prevernal species occur in this faciation, but in the areas intervening between the mats of sod *Draba reptans, D. cuneifolia, Viola Kitaibeliana* var. *Rafinesquii, Claytonia virginica* and *Anemone caroliniana* may blossom in February and March. These are followed in early April by *Corydalis micrantha* var. *micrantha, C. micrantha* var. *australis, Androsace occidentalis*, and *Allium Drummondii*. Near the rock outcrops where the soil layer is very thin *Arenaria stricta* var. *texana* and *Lesquerella ovalifolia* var. *alba* (the latter only in the limestone area) often grow abundantly.

The vernal aspect consists of numerous species, many of which continue to blossom well into the summer. Plants of xeric habitats, as *Hymenoxys linearifolia, Arenaria patula, Neobessya missourienis* and *Marshallia caespitosa*, commonly form societies among rocks and on gravelly mounds. Habitats of a slightly less xeric nature support such species as *Plantago Purshii, P. rhodosperma, Thelesperma intermedium* and *Scutellaria parvula* var. *australis*. Plants characteristic of eroding banks along ravines, or other disclimax spots, are *Lomatium foeniculaceum, Solanum carolinense, Oenothera missouriensis* var. *missouriensis* and *Tribulus terrestris*. Those most common in moderately moist prairies are *Linaria canadensis, Oxalis stricta, Penstemon Cobaea, P. oklahomensis, Collinsia violacea, Castilleja indivisa, Daucus pusillus, Allium canadense* var. *mobilense, Coreopsis grandiflora* var. *grandiflora, Echinacea angustifolia, Gaillardia pulchella, Cacalia plantaginea, Erigeron annuus* and *Baptisia leucophaea*.

The estival species of the tall-grass prairie are for the most part deeply

rooted, reaching moisture of the subsoil. These plants, indicative of dry gravelly soils, are *Palafoxia callosa* var. *calloso*, *Aplopappus ciliatus*, *Chrysopsis pilosa*, *Opuntia humifusa* and *Hymenopappus scabiosiaeus*. In the slightless xeric regions are *Dalea purpureum*, *D. multiflora*, *D. candida*, *Baptisia australis* var. *minor*, *Yucca glauca* var. *glauca*, *Oenothera serrulata*, *Polytaenia Nuttallii*, *Asclepias viridis*, *A. capricornu* and *Linum Lewisii* var. *pratense*. Low meadows of moist rich soil contain such summer flowering plants as *Amorpha canescens* var. *canescens*, *A. fruticosa* var. *angustifolia*, *Astragalus canadensis*, *Melilotus officinalis*, *Psoralea tenuiflora*, *Euphorbia dentata*, *E. marginata*, *E. corollata* var. *corollata*, *Callirhoe involucrata* var. *involucrata*, *C. alcaeoides*, *Physalis pumila*, *Salvia azurea* var. *grandiflora*, *Monarda citriodora*, *Plantago virginica* var. *virginica* and *Rudbeckia amplexicaulis*.

The serotinal aspect of the drier prairies consists primarily of *Aster ericoides*, *A. praealtus*, *Mentzelia oligosperma*, *Eryngium Leavenworthii*, *Solidago altissima*, *S. nemorolis* var. *decemflora* and *S. rigida*, while the plants most common in the moist low meadows are *Carex Frankii*, *Cyperus ovularis* var. *ovularis*, *Tovara virginiana* var. *virginiana*, *Liatris aspera* var. *intermedia*, *Liatris squarrosa* var. *glabra*, *Helianthus hirsutus* var. *hirsutus*, *H. mollis*, *Heterotheca latifolia*, *and Vernonia Baldwini* var. *interior*.

NONARABLE FLOOD PLAINS

The principal climax of the low flood plains vegetation is the *Quercus-Ulmus* faciation, with *Quercus Muhlenbergii*, *Q. Shumardii* var. *Schneckii* and *Ulmus americana* as the dominants. There are places in which two or more of these are replaced, at least partially, by *Quercus macrocarpa*, *Juglans nigra*, *Carya illinoensis* or *Populus deltoides*, as dominants. In addition to these, there is likely to be a good growth of *Salix nigra* and *Cephalanthus occidentalis* along the stream margins where the water table is shallow. *Alnus maritima* is limited in its growth to the low banks of two streams, Sheep Creek and Byrds Mill Creek, in the southern part of the county.

The seasonal aspect on the forest floor of the flood plains is limited to a few shade-tolerant species. Among the prevernal species are *Viola missouriensis*, *V. triloba* var. *dilatata*, *Polygonatum canaliculatum*, and in the southern portion, *Podophyllum peltatum*, which appears in definite local communities.

Among the vernal species are most of the above-mentioned prevernals, and, in addition, such later flowering plants as *Parietaria pensylvanica*, *Arisaema Dracontium*, *Valerinella radiata*, *Fragaria virginiana* var. *virginiana*, *Geum canadense* var. *camporum*, *Desmodium Dillenii*, *Cicuta maculata*, *Sanicula canadensis* var. *canadensis*, *S. gregaria* and *Senecio obovatus* var. *rotundus*.

The estival aspect includes *Phryma leptostachya* var. *leptostachya*, *Physalis heterophylla* var. *heterophylla*, *Urtica chamydryoides*, *Mentha spicata*, *Taenidia integerrima*, *Zizia aurea*, *Commelina erecta* var. *erecta*, *Desmodium glutinosum*, *Silene stellata* var. *scabrella* and *Salvia lyrata*. Many of the low or climbing vines are in flower or fruit during this season. Some of these are *Cocculus carolinus*, *Menispermum canadense*, *Smilax Bona-nox*, *Vitis cinerea* and *Parthenocissus quinquefolia*. Also, the semiparasitic *Phoradendron*

flavescens, growing rather abundantly on the branches of *Ulmus americana* and *Ulmus rubra*, and occasionally on some of the other trees, flowers at this time.

The most prominent serotinal plants of the low flood plain forest floor, are *Elephantopus carolinianus*, *Eupatorium coelestinum*, *Bidens bipinnata*, *Aster sagittifolius*, *Lobelia cardinalis* and *Agrimonia pubescens*. Occasionally species that are usually found on open slopes, such as *Aster exilis*, *Solidago ulmifolia*, *Xanthium italicum* and *Eupatorium serotinum*, are also found in these low shaded areas.

DISCLIMAXES OF ABANDONED FIELDS

Approximately 40 percent of the county is composed of soils that have been disturbed by cultivation of crops. However, at present, it is estimated that only one-half of this area remains in cultivation, thus leaving a good portion of the county acreage as abandoned fields. Many of these fields are in early stages of succession. Most small flood plains were abandoned as areas for field crops, due to repeated overflows, or because the tracts were so small that farming was unprofitable. Many fields were abandoned on high plains and slopes because of extreme erosion, and as a result of recent tendencies toward stock farming in the county.

Flood Plains.—The field crops that are cultivated on the flood plains must compete constantly with many weedy species. Some of the most common of these are *Sorgum halepense*, *Setaria geniculata*, *Parietaria pensylvanica*, *Acalypha virginica*, *Euphorbia dentata*, *E. maculata*, *Physalis pendula*, *Helianthus mollis* var. *mollis*, *H. annuus*, *Rudbeckia amplexicaulis*, *R. bicolor*, *Ratibida columifera* and *Xanthium pensylvanicum*. These plants, therefore, represent the major part of the initial disclimax succession after these fields are abandoned.

The prevernal aspect often includes *Descurainia pinnata* var. *brachycarpa*, *Capsella bursa-pastoris*, *Chaerophyllum procumbens*, *Lamium amplexicaule*, *Galium Aparine*, *Erigeron philadelphicus* and *Senecio obovatus* var. *rotundus*. Where succession has progressed far enough, some woody species such as *Cephalanthus occidentalis*, in very moist places, and *Smilax Bona-nox* in sandy loam, have replaced some of the above herbaceous species.

Common among the vernal plants, of very sandy soils are *Cnidoscolus texanus*, *Physalis longifolia* and *P. pendula*. while in sandy loam are such plants as *Phytolacca americana*, *Melilotus officinalis*, *Vicia minutiflora*, *Oenothera lacinata* var. *laciniata*, *Torilis japonica*, *Echinacea atrorubens* var. *atrorubens* and *ratibida columnifera*.

Some of the more common estival species of the sandy soils are *Sorgum halepense*, *Paspalum distichum*, *Echinochloa pungens* var. *pungens*, *Elymus canadensis*, *Setaria glauca* var. *glauca*, *S. geniculata*, *Carex Frankii*, *Cyperus uniflorus*, *Diodia teres*, *Juncus biflorus*, *Physalis longifolia*, *P. pendula*, *Solanum americanum*, *Centaurea americana*, *Rudbeckia bicolor*, and in the rich moist clay loam *Juncus Dudleyi*, *J. Torreyi*, *Parietaria pensylvanica*, *Polygonum hydropiperoides* var. *hydropiperoides*, *P. pensylvanicum* var. *laevigatum*, *Physalis heterophylla* var. *heterophylla*, *Ruellia strepens*, *Helianthus*

annuus, Lactuca canadensis var. *canadensis* and *Rudbeckia amplexicaulis.* Occasional plants of such species as *Helianthus mollis* var. *mollis* and *Xanthium pensylvanicum* flower at this time but most of these flower and develop fruit through the autumn.

Some of the more common serotinal plants of the low, sandy, and abandoned fields are *Sorghastrum nutans, Echinochloa pungens* var. *pungens, Andropogon virginicus* var. *virginicus, Euphorbia dentata, E. maculata, Ludwigia hirtella, Eustoma Russelliana, Aster ericoides, A. exilis, Gaillardia fastigata* and *Heterotheca latifolia.* Those growing in rich clay loam often include *Conyza canadensis* var. *canadensis* and *Eupatorium serotinum,* with *Cocculus carolinus* occasionally twining about these.

High Plains and Slopes.—Among the abandoned field disclimaxes of high plains and slopes are those of sandy soil which are restricted mostly to the northwestern portion, and those of rocky or gravelly soil found largely in the eastern and northeastern portions. The dry exposed areas contain the grasses, *Andropogon saccharoides, A. ternarius* var. *ternarius, Aristida oligantha, Agrostis hyemalis, Cenchrus longispinus, Digitaria sanguinalis* var. *sanguinalis,* and *Eleusine indica.* Some rushes that are often associated with these are *Juncus interior* and *J. Dudleyi.* Old fields with a little more soil moisture usually contain *Bromus japonicus* var. *japonicus, Elymus virginicus* var. *virginicus, Eragrostis oxylepis* var. *oxylepis, Panicum dichotomiflorum, Setaria geniculata, S. glauca* and *Triodia flava.*

The prevernal aspect of these abandoned fields includes a few small species such as *Stellaria media* var. *media, Capsella bursa-pastoris, Descurainia pinnata* var. *brachycarpa, Draba reptans* var. *reptans, Lepidium virginicum, Lesquerella gracilis* var. *repanda* and *Oxalis stricta.*

Prominent in the vernal flora are *Plantago aristata,* where the soil is badly eroded, and *Rosa foliolosa* on the rocky or gravelly slopes. Commonly growing in dry sandy habitats are *Rumex hastatalus, Cycloloma atriplicifolium, Medicago hispida, Evolvulus nuttallianus, Solanum carolinense, S. rostratum* and *Helianthus petiolaris.* Regions of more moisture, such as depressions along terraces, may contain *Psoralea tenuiflora* and *Erigeron strigosus* var. *strigosus.*

The dry, exposed slopes nearly always contain a good distribution of *Cassia fasciculata* during the summer months. This species is often accompanied in sandy areas by *Froelichia floridana* var. *campestris, Oenothera rhombipetala, Cnidoscolus texanus, Euphorbia dictyosperma* and *Gaillardia lanceolata.* If erosion has progressed to the extent of removing all of the original surface soil, *Aristida oligantha* and *A. purpurea* may constitute the total estival aspect.

Most of the serotinal species found in abandoned fields are the grasses, *Andropogon saccharoides, A. ternarius, Aristida oligantha, Agrostis hyemalis, Cenchrus longispinus, Digitaria sanguinalis* var. *sanguinalis,* and *Eleusine indica.* Associated with these are *Eriogonum annuum, E. longifolium, Lespedeza stipulacea, Aplopappus ciliatus, Solidago ulmifolia,* and *S. mollis* var. *mollis.*

HYDROPHYTIC ZONES

There are in Pontotoc County many farm ponds (most of which occupy less than one acre) also Lake Wintersmith, one mile southeast of Ada, the South Canadian River, the Blue River, and many smaller streams, all contain several aquatic and semiaquatic plant species.

Because of the continuous habitat differences in and around ponds and lakes, the structure of the vegetation can be clearly seen in zonation. Free-floating or partially submerged algae usually occupy an area near the center of ponds and lakes. These are followed by such flowering plants as *Nelumbo lutea, Potamogeton nodosus, Najas guadalupensis* and *Justicia americana* var. *subcoriacea,* which grow at various depths, rooted in the muddy or sandy bottom. They may form dense masses of vegetation in older ponds. The two latter species are entirely submerged, while the others have floating leaves and aerial flowers.

The succeeding zone is characterized by the tall plants *Scirpus validus* var. *creber* and *Typha latifolia* which are rooted in the muddy shallow margins. Associated with these in some ponds is *Lemna minor,* which is a free-floating species but is usually restricted to the margins because of surface waves. Also, in at least two of the larger ponds of the eastern part of the county, *Sagittaria falcata* is a part of this marginal zone.

The land margin surrounding ponds usually contains a zone including several sedges, rushes, and grasses intermixed with a few species of forbs. Some of these plants are *Carex Frankii, C. Meadii, C. vulpinoidea, Cyperus acuminatus, C. esculentus, C. setigerus, Juncus diffusissimus, Tripsacum dactyloides, Paspalum distichum, P. floridanum, Phalaris caroliniana, Cicuta maculata* and *Polygonum lapathifolium* var. *lapathifolium.*

The succeeding zone is marked by a good growth of woody plants. Among these are *Cephalanthus occidentalis, Salix nigra, Cornus florida, C. Drummondii* and *Populus deltoides.*

The final zone is characterized by the climax or subclimax association of the area, therefore is usually oak-hickory or tall-grass prairie, depending on the locality.

The small spring-fed streams of the hills and slopes often contain partly submerged *Nasturtium officinale* var. *officinale* and have small communities of *Equisetum hyemale* var. *affine, E. hyemale* var. *intermedium* and *Woodsia obtusa* growing along the rocky margins or steep banks. Otherwise the vegetation of these habitats was described along with the oak-hickory association, of which they are a part.

Along the sandy bed of the South Canadian River may be found certain species that are for the most part late flowering annuals. Some of these are *Echinochloa pungens* var. *pungens, Eragrostis pectinacea, Leptochloa filiformis, Panicum capillare* var. *capillare, Acnida tamariscina, Conobea multifida, Eclipta alba, Ammania coccinea, Fimbristylis Vahlii, Fuirena simplex, Cyperus erythrorhizos* and *Eleocharis compressa* var. *compressa.* In addition to these annuals there often are early seedling communities of *Salix nigra* and *Populus deltoides* which are almost completely destroyed by spring floods when water spreads over these beds of sand. Another small tree, *Tamarix gallica,* pre-

dominates on some of the beds of sand that are inundated less often. This species has been fairly successful in gaining a foothold over many acres of the bottom along the river.

RELATIONSHIPS OF THE FLORA

Since Pontotoc County is located in the transition area between the tall grass prairie and the oak-hickory forest, floras of both are well represented. With the aid of recent manuals more or less arbitrary groupings were made to show the geographic relationships of this flora. Separate consideration was given to each taxon of specific rank. The groups consist of plants having the following distributional patterns: 1) wide range throughout most of North America, as shown by their being found in several manuals covering different parts of North America; 2) wide range across southern states; 3) wide range in eastern North America; 4) wide range in western North America; 5) wide range in the interior of the United States (especially prairie states); 6) ranging throughout southeastern states; 7) ranging throughout northeastern states; 8) ranging throughout southwestern states; 9) limited mostly to Missouri, Kansas, Oklahoma, and Texas.

Species of Pontotoc County that have a wide range throughout most of North America number 115, representing approximately 16.5 percent of the total flora. These include many cosmopolitan species, such as *Stellaria media* var. *media* and *Geranium carolinianum* var. *carolinianum*. Others that are slightly more limited in range, as *Juncus interior*, occurring from Michigan to Washington and south to Texas, are included in this group.

There are only 24 species, or 3.5 percent of the total, that are considered of wide range throughout only the southern states. Typical representatives of this group are *Andropogon saccharoides*, which occurs from Alabama to Mexico and north to Missouri and Southern California, and *Sibara virginica* which extends from Florida and Mexico to eastern Virginia and southern California.

Approximately 255, or 36.5 percent of the plants of the county, are included in the general range of eastern North America. In this group are most of the forest trees, such as *Quercus Muhlenbergii*, which occurs from northern Florida to eastern Texas and north to Vermont and eastern Nebraska, along with many woodland species, such as *Sanicula canadensis* var. *canadensis*, which occurs from Florida to Texas and north to New Hampshire, Ohio and Missouri. Many prairie species are found in this group. A typical example of such plants is *Bouteloua curtipendula*, which ranges from Connecticut to Ontario, west to Montana and south to Georgia, Texas, and Mexico.

The western range, as considered in this grouping, includes the entire area from the Great Plains westward to the Pacific Ocean. Only 13 species, or 1.9 percent of the total flora, are of this range. Typical of these are *Gaura parviflora* var. *parviflora*, which occurs from Texas to Illinois and west to Washington, and *Ambrosia psilostachya* var. *psilostachya*, which extends from Illinois to Saskatchewan and south to Texas, Mexico and California.

Species that are more or less limited to the Prairie States of the interior number 112, or approximately 16 percent of the total flora. Typical of these

are the species *Vernonia Baldwini* var. *interior*, occurring from Illinois to Minnesota and Nebraska, south to Arkansas and Texas, and *Androsace occidentalis*, with a more extensive range from Ontario to British Columbia, and south to Arkansas, Texas, New Mexico and Arizona. It is not intended that this group includes all prairie species, since many such species are included in other more extensive ranges.

Species that extend throughout the southeastern portion of the United States number 102, or 14.5 percent of the total. This area extends from Florida to Texas and north to southern New England and west to Missouri and Kansas, although several species are included in this group, that do not extend so far northward. Typical of this group are *Viburnum rufidulum* and *Diospyros virginiana* var. *virginiana*, which extends only as far north as Missouri and Tennessee.

Only 8 species, or 1.1 percent of the total flora of the county is considered of northeastern relationships. These consist of such species as *Commelina communis* var. *ludens* which was naturalized in New Jersey and Pennsylvania to Virginia and Kentucky, becoming only partially established in Pontotoc County, and *Carex annectens* var. *xanthocarpa*, indigenous from Maine to southwestern Quebec and south to Virginia and Oklahoma.

Species of the southwestern group number 24, or 3.5 percent of the total flora. These typically range from Texas to Kansas and west to Mexico and Arizona. Representative species of this group are *Solanum elaeagnifolium*, *Centaurea americana* and *Hymenoxys linearifolia*.

A more limited range considered is one including all or portions of Missouri, Kansas, Oklahoma and Texas, with now and then an extension into Colorado, Arkansas or Louisiana. There are approximately 45 species, or 6.5 percent of the county flora that are thus restricted in range. Typical of these are the following: *Oenothera missouriensis* var. *missourienis*, *O. missouriensis* var. *oklahomensis*, *Baptisia australis* var. *minor*, *Cyperus setigerus*, *Tradescentia Tharpii*, *Eriogonum longifolium*, *Rhynchosia latifolia*, *Eryngium Leavenworthii*, *Limnosciadium pinnatum*, *Physalis pendula*, *Collinsia violacea*, *Valerianella stenocarpa* var. *parviflora*, *Chrysopsis pilosa*, *Erigeron tenuis*, *Marshallia caespitosa* and *Palafoxia callosa* var. *callosa*.

List of the Species, Varieties and Forms

PTERIDOPHYTA

EQUISETACEAE

Equisetum hyemale L., var. *affine* (Engelm.) A. A. Eat.

E. hyemale L., var. *intermedium* A. A. Eat.

OPHIOGLOSSACEAE

Botrychium virginianum (L.) Sw., var. *virginianum*

Ophioglossum Engelmanni Prantl (G. T. Robbins 3014; OU)

POLYPODIACEAE

Adiantum Capillus-Veneris L.

Asplenium platyneuron (L.) Oakes

Cystopteris fragilis (L.) Bernh., var. *simulans* (Weatherby) McGregor

Pellaea atropurpurea (L.) Link, var. *atropurpurea*

Polypodium polypodioides (L.) Watt, var. *michauxianum* Weatherby

Woodsia obtusa (Spreng.) Torr.

SPERMATOPHYTA

GYMNOSPERMAE

PINACEAE

Juniperus virginiana L., var. *virginiana*

ANGIOSPERMAE

MONOCOTYLEDONEAE

TYPHACEAE

Typha domingensis Pers.
T. latifolia L.

ZOSTERACEAE

Potamogeton diversifolius Raf.
P. nodosus Poir.

NAJADACEAE

Najas guadalupensis (Spreng.) Magnus

ALISMACEAE

Sagittaria falcata Pursh

GRAMINEAE

Aegilops cylindrica Host., var. *cylindrica*
Agropyron Smithii Rydb.
Agrostis hyemalis (Walt.) BSP.
Alopecurus carolinianus Walt.
Andropogon Gerardi Vitmin, var. *Gerardi*
A. saccharoides Sw.
A. scoparius Michx.
A. ternarius Michx.
A. virginicus L., var. *virginicus*
A. virginicus L. var. *abbreviatus* (Hack.) Fern. & Grisc.
Aristida adscensionis L.
A. oligantha Michx.
A. purpurascens Poir.
A. purpurea Nutt.
Bouteloua curtipendula (Michx.) Torr.
B. hirsuta Lag., var. *hirsuta*
B. hirsuta Lag., var. *pectinata* (Feath.) Cory
Bromus catharticus Vahl.
B. japonicus Thunb., var. *japonicus*
B. japonicus Thunb., var. *porrectus* Hack.
B. pratensis Ehrh.
B. secalinus L.
B. tectorum L.
Buchloe dactyloides (Nutt.) Engelm.
Cenchrus longispinus (Hack.) Fern.
C. pauciflorus Benth.
Chloris verticillata Nutt.
Cynodon dactylon (L.) Pers.
Digitaria Ischaemum (Schreb.) Muhl., var. *Ischaemum*
D. sanguinalis (L.) Scop., var. *sanguinalis*
Echinochloa pungens (Poir.) Rydb., var. *pungens*
E. pungens (Poir.) Rydb., var. *Wiegandii* Fassett
Eleusine indica (L.) Gaertn.
Elymus canadensis L.
E. canadensis L., forma *glaucifolius* (Muhl.) Fern.
E. virginicus L., var. *virginicus*
E. virginicus L., var. *virginicus*, forma *hirsutiglumis* (Scribn.) Fern.
E. virginicus L., var. *glabrifolius* (Vasey) Bush, forma *australis* (Scribn. & Ball) Fern.
Eragrostis capillaris (L.) Nees
E. intermedia Hitchc.
E. megastachya (Koel.) Link
E. oxylepis (Torr.) var. *oxylepis*
E. pectinacea (Michx.) Scribn.
E. pilosa (L.) Beauv.
E. poaeoides Beauv. ex Roem. & Schult.
E. spectabilis (Pursh) Steud., var. *sparsihirsuta* Farw.
E. trichodes (Nutt.) Nash, var. *trichodes*
Glyceria striata (Lam.) Hitchc., var. *striata*
Hordeum pusillum Nutt.
Koeleria cristata (L.) Pers.
Leptochloa filiformis (Lam.) Beauv.
Leersia virginica Willd., var. *virginica*

Limnodea arkansana (Nutt.) L. H. Dewey
Lolium multiflorum Lam.
Melica nitens Nutt.
Muhlenbergia capillaris (Lam.) Trin. (G. T. Robbins 2263; OU)
Panicum anceps Michx., var. *anceps*
P. capillare L., var. *capillare*
P. capillare L., var. *occidentale* Rydb.
P. dichotomiflorum Michx., var. *dichotomiflorum*
P. lanuginosum Ell., var. *fasciculatum* (Torr.) Fern.
P. lanuginosum Ell., var. *Lindheimeri* (Nash) Fern.
P. malacophyllum Nash (G. T. Robbins 2279; OU)
P. obtusum HBK. (G. T. Robbins 3097; OU)
P. oligosanthes Schultes, var. *oligosanthes*
P. oligosanthes Schultes, var. *Helleri* (Nash) Fern.
P. oligosanthes Schultes, var. *Scribnerianum* (Nash) Fern.
P. scoparium Lam.
P. sphaerocarpon Ell., var. *sphaerocarpon*
P. virgatum L., var. *virgatum*
Paspalum bifidum (Bertol.) Nash, var. *bifidum* (U. T. Waterfall 5684; OU)
P. ciliatifolium Michx., var. *Muhlenbergii* (Nash) Fern.
P. dilatatum Poir. (G. T. Robbins 2680; OU)
P. distichum L.
P. floridanum Michx. var. *floridanum*
P. pubiflorum Rupr., var. *glabrum* Vasey
Phalaris caroliniana Walt.
Poa bulbosa L.
Setaria geniculata (Lam.) Beauv.
S. glauca (L.) Beauv.
S. viridis (L.) Beauv., var. *viridis*
Sorghastrum nutans (L.) Nash
Sorgum halepense (L.) Pers.
Sphenopholis obtusata (Michx.) Scribn., var. *obtusata*
S. obtusata (Michx.) Scribn., var. *lobata* (Trin.) Scribn.
Sporobolus canovirens Nash (M. Hopkins & Van Valkenburgh 5555; OU)
S. cryptandrus (Torr.) Gray
Stipa leucotricha Trin.
Triodia flava (L.) Hitchc.
T. pilosa (Buckl.) Merr.
Tripsacum dactyloides L.
Uniola latifolia Michx.
Vulpia octoflora (Walt.) Rydb.

CYPERACEAE

Bulbostylis capillaris (L.) C. B. Clark, var. *crebra* Fern.
Carex annectens Bickn., var. *xanthocarpa* (Bickn.) Wieg.
C. austrina (Small) Mack.
C. bicknellii Britton.
C. blanda Dewey
C. Frankii Kunth
C. granularis Muhl.
C. Meadii Dewey
C. Muhlenbergii Schkuhr., var. *Muhlenbergii*
C. Muhlenbergii Schkuhr., var. *enervis* Boott
C. oligocarpa Schkuhr.
C. physorhyncha Liebm.
C. retroflexa Muhl.
T. texensis (Torr.) Bailey (G. T. Robbins 2951; OU)
C. vulpinoidea Michx., var. *vulpinoidea*
Cyperus acuminatus Torr. & Hook.
C. erythrorhizos Muhl.
C. esculentus L., var. *esculentus*
C. filiculmis Vahl., var. *filiculmis*
C. odoratus L.
C. ovularis (Michx.) Torr., var. *ovularis*
C. ovularis (Michx.) Torr., var. *sphaericus* Chapm.
C. setigerus Torr. & Hook.
C. strigosus L., var. *strigosus*
C. uniflorus Torr. & Hook.
C. virens Michx.
Eleocharis macrostachya Britt.
E. montevidensis Kunth
Fimbristylis interior Britton
F. Vahlii (Lam.) Link
Fuirena simplex Vahl
Rhynchospora capitellata (Michx.) Vahl. (W. T. Penfound P-343a; OU)
Scirpus lineatus Michx.
S. validus Vahl, var. *creber* Fern.

ARACEAE

Arisaema Dracontium (L.) Schott.

LEMNACEAE

Lemna minor L.

COMMELINACEAE

Commelina communis L., var. *ludens* (Miquel) Clarke (G. T. Robbins 2611; OU)
C. erecta L., var. *erecta*
C. erecta L., var. *angustifolia* (Michx.) Fern., forma *crispa* (Woot.) Fern.
Tradescantia ohiensis Raf.
T. Tharpii Anders. & Woodson

JUNCACEAE

Juncus acuminatus Michx.
J. biflorus Ell.
J. brachycarpus Engelm.
J. brachyphyllus Wiegand
J. diffusissimus Buckl.
J. Dudleyi Wiegand
J. interior Wiegand
J. nodatus Coville, var. *robustus* (Engelm.) Coville
J. Torreyi Coville
J. validus Coville

LILIACEAE

Allium canadense L., var. *canadense*
A. canadense L., var. *mobilense* (Regel) Ownbey
A. Drummondi Regel
Androstephium coeruleum (Scheele) Greene
Camassia scilloides (Raf.) Cory
Erythronium albidum Nutt., var. *mesochoreum* (Knerr) Rickett
Nothoscordum bivalve (L.) Britton
Polygonatum canaliculatum (Muhl.) Pursh
Smilax Bona-nox L., var. *Bona-nox*
S. glauca Walt., var. *glauca*
S. glauca Walt., var. *leurophylla* Blake
S. rotundifolia L.
S. tamnoides L., var. *hispida* (Muhl.) Fern.
Yucca glauca Nutt., var. *glauca*

AMARYLLIDACEAE

Agave lata Shinners (G. T. Robbins 3094; OU)
Hypoxis hirsuta (L.) Covil'e

IRIDACEAE

Nemastylis geminiflora Nutt.
Sisyrinchium angustifolium Mill.
S. campestre Bickn.

ORCHIDACEAE

Corallorhiza Wisteriana Conrad
Epipactis gigantea Dougl.
Spiranthes gracilis (Bigel.) Beck (G. T. Robbins 2268; OU)

DICOTYLEDONEAE

SALICACEAE

Populus alba L.
P. deltoides Marsh.
Salix nigra Marsh.

JUGLANDACEAE

Carya cordiformis (Wang.) K. Koch
C. illinoensis (Wang.) K. Koch
C. texana Buckl.
C. tomentosa (Poir.) Nutt.
Juglans nigra L.

BETULACEAE

Alnus maritima (Marsh.) Muhl.

FAGACEAE

Quercus falcata Michx., var. *falcata*
Q. falcata Michx., var. *triloba* (Michx.) Nutt.
Q. macrocarpa Michx.
Q. marilandica Muench.
Q. muhlenbergii Engelm.
Q. palustris Muench.
Q. prinoides Willd.
Q. rubra L., var. *rubra*
Q. Shumardii Buckl., var. *schneckii* (Britton) Sarg.
Q. stellata Wang., var. *stellata*
Q. velutina Lam., var. *velutina*
Q. velutina Lam., var. *velutina*, forma *macrophylla* (Dippel) Trel.

ULMACEAE

Celtis laevigata Willd., var. *laevigata*
Ulmus alata Michx.
U. americana L.
U. rubra Muhl.

MORACEAE

Broussonetia papyrifera (L.) Vent.
Maclura pomifera (Raf.) Schneider
Morus rubra L.

URTICACEAE

Parietaria pensylvanica Muhl.
Pilea pumila (L.) Gray, var. *deamii* (Lunell) Fern. (G. T. Robbins 3189; OU)
Urtica chamaedryoides Pursh

LORANTHACEAE

Phoradendron flavescens (Pursh) Nutt.

POLYGONACEAE

Eriogonum annuum Nutt.
E. longifolium Nutt.
Polygonum convolvulus L., var. *Convolvulus*
P. cristatum Engelm. & Gray
P. Hydropiper L.
P. hydropiperoides Michx., var. *hydropiperoides*
P. hydropiperoides Michx., var. *Bushianum Stanford*
P. lapathifolium L., var *lapathifolium*
P. orientale L.
P. pensylvanicum L., var. *laevigatum* Fern.
P. Persicaria L., var. *Persicaria*
P. prolificum (Small) Robinson
P. punctatum, var. *parviflorum* Fassett
Rumex altissimus Wood
R. crispus L.
R. hastatulus Baldw.
R. verticillatus L.
Tovara virginiana (L.) Raf., var. *virginiana*

CHENOPODIACEAE

Chenopodium album L. (G. T. Robbins 3205; OU)
C. carintum R. Br.
C. pallescens Standl.
C. pratericola Rydb., var. *pratericola*
Cycloloma atriplicifolium (Spreng.) Coult.

AMARANTHACEAE

Acnida tamariscina (Nutt.) Wood
Amaranthus graecizans L. U. T. Waterfall 8390; OU)
A. spinosus L.
Froelichia floridana (Nutt.) Moq. var. *campestris* (Small) Fern.
Iresene rhizomotosa Standl. (G. T. Robbins 2761; OU)

NYCTAGINACEAE

Mirabilis albida (Walt.) Heimerl, var. *lata* Shinners
M. linearis (Pursh) Heimerl.
M. nyctaginea (Michx.) MacM.

PHYTOLACCACEAE

Phytolacca americana L.

AIZOACEAE

Mollugo verticillata L.

PORTULACACEAE

Claytonia virginica L.
Portulaca mundula I. M. Jtn.. (U. T. Waterfall 8391; OU)

CARYOPHYLLACEAE

Arenaria patula Michx., forma *media* Steyerm.
A. patula Michx., forma *pitcheri* (Nutt.) Steyerm.
A. stricta Michx., var. *texana* Robinson
Cerastium brachypodium (Engelm.) Robinson
C. viscosum L.
Silene antirrhina L. (G. T. Robbins 2946; OU)
S. stellata (L.) Ait. f., var. *scabrella* (Nieuwl.) Palm. & Steyerm.
Stellaria media (L.) Cyrill, var. *media*
S. nuttallii T. & G.

ILLECEBRACEAE

Paronychia virginica Spreng., var. *scoparia* (Small) Cory

NYMPHAEACEAE

Nelumbo lutea (Willd.) Pers.

RANUNCULACEAE

Anemone caroliniana Walt.
A. caroliniana Walt., forma *violacea* Clute
A. decapetala Ard.
Clematis pitcheri T. & G.
Delphinium Ajacis L.
D. tricorne Michx.
D. virescens Nutt., var. *virescens*
Ranunculus fascicularis Muhl., var. *apricus* (Greene) Fern.

MENISPERMACEAE

Cocculus carolinus (L.) DC.
Menispermum canadense L.

BERBERIDACEAE

Podophyllum peltatum L.

PAPAVERACEAE

Argemone intermedia Sweet

FUMARIACEAE

Corydalis crystallina Engelm.
C. micrantha (Engelm.) Gray, var. *micrantha*
C. micrantha (Engelm.) Gray, var. *australis* (Chapm.) Shinners

CAPPARIDACEAE

Polanisia trachysperma T. & G.

CRUCIFERAE

Arabis canadensis L. (G. T. Robbins 3004; OU)
Brassica juncea (L.) Coss.
B. Kaber (DC.) Wheeler, var. *pinnatifida* (Stokes) Wheeler
Camelina microcarpa Andrz.
Capsella bursa-pastoris (L.) Medic., var. *bursa-pastoris*
Cardamine parviflora L., var. *arenicola* (Britt.) O. E. Schultz. (Van Valkenburgh 10a; OU)
Descurainia pinnata (Walt.) Britt., var. *brachycarpa* (Richards.) Fern.
Draba brachycarpa Nutt.
D. cuneifolia Nutt., var. *cuneifolia*
D. reptans (Lam.) Fern., var. *reptans*
Erysimum asperum DC., var. *asperum*
E. repandum L.
Lepidium densiflorum Schrad.
L. virginicum L., var. *virginicum*
Lesquerella gracilis (Hook.) Wats., var. *repanda* (Nutt.) Payson
L. ovalifolia Rydb., var. *alba* Goodman
Nasturtium officinale R. Br., var. *officinale*
Rorippa islandica (Oeder ex Muir) Borbas, var. *Fernaldiana* Butt. & Abbe
R. sessiliflora (Nutt.) Hitchc.
Sibara virginica (L.) Rollins
Thlaspi arvense L.

CRASSULACEAE

Sedum pulchellum Michx.

SAXIFRAGACEAE

Penthorum sedoides L. (G. T. Robbins 2300; OU)

PLATANACEAE

Platanus occidentalis L.

ROSACEAE

Agrimonia pubescens Wallr.
Crataegus crus-galli L.
C. mollis (T. & G.) Scheele
C. viridis L., var. *lutensis* (Sarg.) Palmer
Fragaria virginiana Duchesne, var. *virginiana*
Geum canadense Jacq. var. *camporum* (Rydb.) Fern. & Weath.
Potentilla simplex Michx., var. *simplex* (G. J. Goodman 5467; OU)
Prunus americana Marsh., var. *lanata* Sudw.
P. angustifolia Marsh., var. *angustifolia*
P. gracilis Engelm. & Gray
P. mexicana Wats.
P. serotina Ehrh.
Rosa carolina L., var. *carolina*, forma *glandulosa* (Crepin) Fern.
R. foliolosa Nutt.
R. setigera Michx., var. *tomentosa* T. & G.
Rubus trivialis Michx., var. *trivialis*
Sanguisorba annua Nutt.

LEGUMINOSAE

Acacia angustissima (Mill.) Kuntze, var. *hirta* (Nutt.) Robinson
Amorpha canescens Pursh, var. *canescens*
A. fruticosa L., var. *angustifolia* Pursh
Apios americana Medic., var. *americana* (G. T. Robbins 3108; OU)
Astragalus canadensis L., var. *canadensis*
A. caryocarpus Ker
A. nuttallianus DC.
Baptisia australis (L.) R. Br., var. *minor* (Lehm.) Fern.
B. leucantha T. & G.
B. leucophaea Nutt., var. *leucophaea*
B. sphaerocarpa Nutt.
Cassia fasciculata Michx., var. *fasciculata*
Cercis canadensis L., var. *canadensis*
C. canadensis L., var. *canadensis*, forma *glabrifolia* Fern.
Clitoria mariana L.
Crotalaria sagittalis L., var. *sagittalis*
Dalea aurea Nutt.
D. candida Willd.
D. multiflora (Nutt.) Shinners
D. purpurea Vent.
Desmanthus illinoensis (Michx.) MacM.
D. leptolobus T. & G.
Desmodium canescens (L.) DC.
D. ciliare (Muhl.) DC., var. *ciliare*
D. Dillenii Darl.
D. glutinosum (Muhl. ex Willd.) Wood
D. sessilifolium (Torr.) T. & G.
Galactia volubilis (L.) Britt., var. *mississippiensis* Vail
Gleditsia triacanthos L.
Glottidium vesicarium (Jacq.) Harper
Indigofera leptosepala Nutt.
Krameria secundiflora DC.
Lathyrus pusillus Ell.
Lespedeza repens (L.) Bart.
L. stipulacea Maxim.
L. Stuevei Nutt., var. *Stuevei*
L. virginica (L.) Britt.
Lotus americanus (Nutt.) Bisch.
Medicago hispida Gaertn.
M. lupulina L., var. *lupulina*
M. minima L., var. *minima*
M. sativa L.
Melilotus alba Desv.
M. officinalis (L.) Lam.
Neptunia lutea (Leavenw.) Benth., var. *lutea*
Oxytropis Lambertii Pursh
Psoralea esculenta Pursh
P. tenuiflora Pursh
Rhynchosia latifolia L.
Robinia Pseudo-Acacia L.
Schrankia Nuttallii (DC.) Standl.
Sophora affinis T. & G.
Strophostyles helvola (L.) Ell., var. *helvola*
Stylosanthes biflora (L.) BSP., var. *hispidissima* (Michx.) Pollard & Ball (G. T. Robbins 2518; OU)
Tephrosia virginiana (L.) Pers., var. *virginiana*
Trifolium repens L.
Vicia dasycarpa Ten.
V. hirsuta (L.) S. F. Gray
V. minutiflora Dietr.
V. villosa Roth.

LINACEAE

Linum Lewisii Pursh, var. *pratense* Norton
L. medium (Planch.) Britton, var. *texanum* (Planch.) Fern.
L. rigidum Pursh, var. *Berlandieri* (Hook.) T. & G. (G. J. Goodman 5447; OU)

OXALIDACEAE

Oxalis corniculata L., var. *Langloisii* (Small) Wieg.
O. stricta L.
O. violacea L., var. *violacea*

GERANIACEAE

Geranium carolinianum L., var. *carolinianum*

ZYGOPHYLLACEAE

Kallstroemia intermedia Rydb.
Tribulus terrestris L.

EUPHORBIACEAE

Acalypha gracilens Gray, var. *monococca* Engelm.
A. ostryaefolia Riddell
A. virginica L.
Cnidoscolus texanus (Muell. Arg.) Small
Croton capitatus Michx.
C. glandulosus L., var. *septentrionalis* Muell. Arg.
C. monanthogynus Michx.
Euphorbia bicolor Engelm. & Gray
E. corollata L., var. *corollata*
E. dentata Michx.
E. dentata Michx., forma *cophosperma* (Engelm.) Fern.
E. dictyosperma Fisch & Mey.
E. heterophylla L.
E. hexagona Nutt.
E. maculata L.
E. marginata Pursh
E. missurica Raf., var. *missurica*
E. serpens HBK.
E. supina Raf.
Phyllanthus polygonoides Nutt. (G. T. Robbins 2285; OU)
Tragia urticifolia Michx.

ANACARDIACEAE

Rhus aromatica Ait., var. *serotina* (Greene) Rehder
R. copallina L., var. *latifolia* Engler
R. glabra L., var. *glabra*
R. radicans L., var. *radicans*

CELASTRACEAE

Celastrus scandens L. (U. T. Waterfall 7978; OU)
Euonymus atropurpureus Jacq.

ACERACEAE

Acer Negundo L., *texanum* Pax

HIPPOCASTANACEAE

Aesculus glabra Willd., var. *Sargentii* Rehd.

SAPINDACEAE

Sapindus Drummondii H. & A.

RHAMNACEAE

Berchemia scandens (Hill) K. Koch
Ceanothus americanus L., var. *Pitcheri* T. & G.
C. ovatus Desf., var. *pubescens* (S. Wats.) Soper
Rhamnus caroliniana Walt., var. *mollis* Fern.

VITACEAE

Ampelopsis arborea (L.) Koehne
A. cordata Michx.
Parthenocissus quinquefolia (L.) Planch
Vitis cinerea Engelm.
V. Linsecumii Buckl., var. *glauca* Munson
V. vulpina L.

MALVACEAE

Abutilon Theophrasti Medic.
Callirhoe alcaeoides (Michx.) Gray
C. digitata Nutt., var. *stipulata* Waterfall
C. involucrata (Nutt. ex Torr.) Gray, var. *involucrata*
Sida procumbens Sw. (U. T. Waterfall 8387; OU)
S. spinosa L.

GUTTIFERAE

Ascyrum hypericoides L., var. *multicaule* (Michx.) Fern. (G. T. Robbins 2303; OU)
Hypericum punctatum Lam., var. *pseudomaculatum* (Bush) Fern.
H. sphaerocarpum Michx.

TAMARICACEAE

Tamarix gallica L.

CISTACEAE

Lechea tenuifolia Michx., var. *occidentalis* Hodg.
L. villosa Ell., var. *villosa*

VIOLACEAE

Viola kitaibeliana Roem. & Schultz, var. *rafinesquii* (Greene) Fern.
V. missouriensis Greene
V. pedatifida G. Don
V. sagittata Ait. (G. T. Robbins 2334; OU)
V. tricolor L.
V. triloba Schwein., var. *dilatata* (Ell.) Brainerd

PASSIFLORACEAE

Passiflora lutea L., var. *glabriflora* Fern. (G. T. Robbins 3099; OU)

LOASACEAE

Mentzelia oligosperma Nutt.

CACTACEAE

Echinocereus reichenbachii (Tersch.) Haage
Neobessya missouriensis (Sweet) Br. & Rose
Opuntia humifusa Raf.

LYTHRACEAE

Ammannia coccinea Rothb.
Cuphea petiolata (L.) Koehne (G. T. Robbins 2790; OU)
Lythrum lanceolatum Ell.
Rotala ramosior (L.) Koehne, var. *interior* Fern. & Grisc.

ONAGRACEAE

Gaura biennis L., var. *pitcheri* Pickering ex T. & G.
G. filiformis Small (M. Hopkins 5556; OU)
G. parviflora Dougl., var. *parviflora*
G. parviflora Dougl., var. *parviflora*, forma *glabra* Munz
G. suffulta Engelm., var. *suffulta*
Jussiaea repens L., var. *glabrescens* Ktze.
Ludwigia alternifolia L., var. *alternifolia*
L. hirtella Raf.
Oenothera laciniata Hill, var. *laciniata*
O. linifolia Nutt.
O. missouriensis Sims, var. *missouriensis*
O. missouriensis Sims, var. *oklahomensis* (Norton) Munz
O. rhombipetala Nutt.
O. serrulata Nutt.
O. speciosa Nutt.
O. triloba Nutt.
Stenosiphon linifolius (Nutt.) Britton

UMBELLIFERAE

Anethum graveolens L.
Bifora americana (DC.) Wats.
Chaerophyllum procumbens (L.) Crantz
C. tainturieri Hook.
var. *tainturieri*
C. texanum C. & R.
Cicuta maculata L.
Cryptotaenia canadensis (L.) DC.
Daucus pusillus Michx.
Eryngium leavenworthii T. & G.
E. yuccifolium Michx., var. *synchaetum* Gray ex Coult. & Rose
Limnosciadum pinnatum (DC.) Math. & Const.
Lomatium foeniculaceum (Nutt.) Coult. & Rose
Polytaenia nuttalli DC., var. *nuttallii*
Ptilimnium nuttallii (DC.) Britton
Sanicula canadensis L., var. *canadensis*
S. gregaria Bicknell
Spermolepis divaricata (Walt.) Britton
S. echinata (Nutt.) Heller
S. inermis (Nutt.) Math. & Const.
Taenidia integerrima (L.) Drude
Torilis japonicus (Houtt.) DC.
Zizia aurea (L.) Koch.

CORNACEAE

Cornus drummondii C. A. Meyer
C. florida L.

ERICACEAE

Vaccinium arboreum Marsh., var. *arboreum*

PRIMULACEAE

Androsace occidentalis Pursh
Dodecatheon meadia L., var. *meadia*, forma *sedens* Fassett
Samolus parviflorus Raf.

SAPOTACEAE

Bumelia lanuginosa (Michx.) Pers., var. *oblongifolia* (Nutt.) Clark

EBENACEAE

Diospyros virginiana L., var. *virginiana*

OLEACEAE

Forestiera pubescens Nutt., var. *pubescens* (Aven & Ruth Nelson & G. J. Goodman 5491; OU)
Fraxinus americana L., var. *americana*

LOGANIACEAE

Polypremum procumbens L.

GENTIANACEAE

Centaurium beyrichii (T. & G.) Robinson
Eustoma russelianum (Hook.) Griseb.
Sabatia angularis (L.) Pursh
S. angularis (L.) Pursh, forma *albiflora* (Raf.) House
S. campestris Nutt.

APOCYNACEAE

Amsonia ciliata Walt., var. *texana* (Gray) Coulter
Apocynum cannabinum L., var. *cannabinum*

ASCLEPIADACEAE

Ampelamus albidus (Nutt.) Britt.
Asclepias capricornu Woodson, var. *capricornu*
A. stenophylla Gray (U. T. Waterfall 7983; OU)
A. tuberosa L.
A. tuberosa L., forma *lutea* Clute
A. variegata L.
A. verticillata L.
A. viridiflora Raf., var. *viridiflora*
A. viridis Walt.
Matelea biflora (Raf.) Woodson
M. decipiens (Alexander) Woodson (G. T. Robbins 3010; OU)

CONVOLVULACEAE

Convolvulus sepium L., var. *sepium*
Cuscuta campestris Yuncker
C. cuspidata Engelm.
C. glabrior (Engelm.) Yuncker, var. *pubescens* (Engelm.) Yuncker
C. Gronovii Willd., var. *Gronovii*
C. indecora Choisy
Evolvulus Nuttallianus Schultze
Ipomoea pandurata (L.) G. F. W. Mey.
I. purpurea (L.) Roth. (G. T. Robbins 2750b; OU)

POLEMONIACEAE

Gilia rubra (L.) Heller
Phlox pilosa L., var. *pilosa*

HYDROPHYLLACEAE

Ellisia Nyctelea L.
Phacelia hirsuta Nutt.

BORAGINACEAE

Heliotropium tenellum (Nutt.) Torr.
Lithospermum arvense L.
L. carolinense (Walt.) MacMill.
L. incisum Lehm.
Myosotis macrosperma Engelm.
M. verna Nutt.
Onosmodium occidentale Mackenzie (G. T. Robbins 2802; OU)

VERBENACEAE

Lippia lanceolata Michx., var. *recognita* Fern. & Grisc.
L. nodiflora (L.) Michx.
Verbena bipinnatifida Nutt.
V. bracteata Lag. & Rodr.
V. canadensis (L.) Britton
V. halei Small (G. T. Robbins 2486; OU)
V. simplex Lehm.
V. stricta Vent.
V. urticifolia L., var. *urticifolia*

LABIATAE

Glechoma hederacea L., var. *micrantha* Moricand
Hedeoma drummondii Benth.
H. hispida Pursh
Lamium amplexicaule L.
Marrubium vulgare L.
Mentha spicata L.
Monarda citriodora Cerv. ex Lagasca
M. fistulosa L., var. *mollis* (L.) Benth.
M. punctata L., var. *villicaulis* Pennell
M. virgata Raf.
Prunella caroliniana Mill.
Pycnanthemum albescens T. & G. (G. T. Robbins 2254; OU)
P. tenuifolium Schrad.
P. virginianum (L.) Durand & Jackson
Salvia azurea Lam., var. *grandiflora* Benth.
S. lyrata L.
S. reflexa Hornem.
Satureja arkansana (Nutt.) Briq.
Scutellaria drummondii Benth. (G. T. Robbins 2472; OU)
S. parvula Michx., var. *australis* Fassett
Teucrium canadense L., var. *virginicum* (L.) Eaton

SOLANACEAE

Datura meteloides DC.
D. stramonium L.
Physalis heterophylla Nees, var. *heterophylla*
P. longifolia Nutt.
P. pendula Rydb.
P. pumila Nutt.
Solanum americanum Mill.
S. carolinese L.
S. elaeagnifolium Cav.
S. rostratum Dunal

SCROPHULARIACEAE

Castilleja coccinea (L.) Spreng.
C. indivisa Engelm.
Collinsia violacea Nutt.
Conobea multifida (Michx.) Benth.
Gerardia heterophylla Nutt. (G. T. Robbins 2711; OU)
Linaria canadensis (L.) Dumont, var. *texana* (Scheele) Pennell
Penstemon cobaea Nutt., var. *cobaea*
P. oklahomensis Pennell
Verbascum thapsus L.
Veronica arvensis L.
V. peregrina L., var. *xalapensis* (HBK.) St. John & Warren

BIGNONIACEAE

Campsis radicans (L.) Seem.
Catalpa speciosa Warder

ACANTHACEAE

Dicilptera brachiata (Pursh) Spreng. (G. T. Robbins 2758; OU)
Justicia americana (L.) Vahl., var. *subcoriacea* Fern.
Ruellia humilis Nutt., var. *expansa* Fern. (G. T. Robbins 2583; OU)
R. humilis Nutt., var. *longiflora* (Gray) Fern.
R. strepens L.

PHRYMACEAE

Phryma leptostachya L., var. *leptostachya*

PLANTAGINACEAE

Plantago aristata Michx.
P. lanceolata L.
P. purshii R. & S., var. *Purshii*
P. rhodosperma Dcne.
P. rugelii Dcne.
P. virginica L., var. *virginica*

RUBIACEAE

Cephalanthus occidentalis L., var. *occidentalis*
Diodia teres Walt., var. *setifera* Fern. & Grisc.
Galium aparine L.
G. circaezans Michx., var. *hypomalacum* Fern.
G. pilosum Ait., var. *pilosum*
G. pilosum Ait., var. *puncticulosum* (Michx.) T. & G.
G. virgatum Nutt.
Hedyotis minima (Beck) T. & G.
H. nigricans (Lam.) Fosberg

CAPRIFOLIACEAE

Sambucus canadensis L., var. *canadensis*
S. canadensis L., var. *submollis* Rehd.
Symphoricarpos orbiculatus Moench
Triosteum angustifolium L., var. *angustifolium* (G. T. Robbins 3248; OU)
Viburnum rufidulum Raf.

VALERIANACEAE

Valerianella amarella (Lindl.) Krok
V. radiata (L.) Dufr., var. *radiata*
V. stenocarpa (Engelm.) Krok, var. *parviflora* Dyal

CAMPANULACEAE

Lobelia appendiculata DC.
L. cardinalis L.
L. siphilitica L., var. *siphilitica*
Triodanis biflora (R. & P.) Greene
T. leptocarpa (Nutt.) Nieuwl.
T. perfoliata (L.) Nieuwl.

COMPOSITAE

Achillea lanulosa Nutt.
Actinomeris alternifolia (L.) DC. (G. T. Robbins 2746; OU)
Ambrosia artemisiifolia L., var. *elatior* (L.) Descourtils
A. psilostachya DC., var. *psilostachya*
A. trifida L., var. *texana* Scheele
Antennaria plantaginifolia (L.) Richards, var. *plantaginifolia*
Aphanostephus skirrobasis (DC.) Trel.
Aplopappus ciliatus (Nutt.) DC.
Arctium minus (Hill) Bernh.
Artemisia annua L. (G. T. Robbins 2759; OU)
A. ludoviciana Nutt., var. *mexicana* (Willd.) Fern. (G. T. Robbins 2801; OU)
Aster ericoides L.
A. exilis Ell.
A. praealtus Poir.
A. sagittifolius Wedemeyer, var. *drummondii* (Lindl.) Shinners

Astranthium integrifolium (Michx.) Nutt., var. *integrifolium*
Bidens bipinnata L.
B. frondosa L. (G. T. Robbins 2755; OU)
Cacalia plantaginea (Raf.) Shinners
Centaurea americana Nutt.
Chaetopappa asteroides DC.
Chrysopsis pilosa Nutt.
Cirsium altissimum (L.) Spreng.
C. undulatum (Nutt.) Spreng., var. *undulatum*
Conyza canadensis (L.) Cronq., var. *canadensis*
C. canadensis (L.) Cronq., var. *glabrata* (Gray) Cronq.
Coreopsis grandiflora Hogg., var. *grandiflora*
C. grandiflora Hogg., var. *harveyana* (Gray) Sherff
Cosmos sulphureus Cav.
Croptilon divaricatum (Nutt.) Raf., var. *divaricatum*
Echinacea angustifolia DC.
E. atrorubens Nutt., var. *atrorubens*
E. pallida Nutt.
Eclipta alba (L.) Hassk.
Elephantopus carolinianus Raeuschel
Engelmannia pinnatifida T. & G.
Erigeron annuus (L.) Pers.
E. philadelphicus L., var. *philadelphicus*
E. strigosus Muhl. ex Willd., var. *strigosus*
E. strigosus, var. *beyrichii* (Fisch. & Mey.) Gray
E. strigosus, var. *septentrionalis* (Fern. & Weig.) Fern.
E. tenuis T. & G.
Eupatorium altissimum L.
E. coelestinum L.
E. rugosum Houtt., var. *rugosum* (G. T. Robbins 2748; OU)
E. serotinum Michx.
Evax multicaulis DC., var. *multicaulis*
E. prolifera Nutt. ex DC.
Gaillardia fastigata Greene
G. lanceolata Michx.
G. pulchella Foug.
Gnaphalium obtusifolium L., var. *obtusifolium*
G. purpureum L.
Helenium tenuifolium Nutt.
Helianthus annuus L.
H. hirsutus Raf., var. *hirsutus*
H. maximiliani Schrad. (M. Hopkins & Van Valkenburgh 5557; OU)
H. mollis Lam., var. *mollis*
H. petiolaris Nutt.
Heliopsis helianthoides (L.) Sweet, var. *scabra* (Dunal) Fern.
Heterotheca latifolia Buckl.
Hymenopappus scabiosaeus L'Her.
Hymenoxys linearifolia Hook.
Iva ciliata Willd. (G. T. Robbins 2743; OU)
Krigia dandelion (L.) Nutt.
K. occidentalis Nutt.
Lactuca canadensis L., var. *canadensis*
L. canadensis L., var. *canadensis*, forma *angustata* Wieg.
Liatris aspera Michx., var. *intermedia* (Lundell) Gaiser
L. mucronata DC., var. *mucronata*
L. squarrosa (L.) Michx., var. *glabrata* (Rydb.) Gaiser
Lindheimera texana Gray & Engelm.
Marshallia caespitosa Nutt.
Matricaria matricarioides (Less.) Porter
Palafoxia callosa (Nutt.) T. & G., var. *callosa*
Parthenium hysterophorus L.
Pyrrhopappus carolinianus (Walt.) DC.
P. geiseri Shinners
P. scaposus DC.
Ratibida columnifera (Nutt.) W. & S.
Rudbeckia amplexicaulis Vahl
R. bicolor Nutt. sensu Fern.
R. serotina Nutt., var. *sericea* (T. V. Moore) Fern. & Schub. (Smith & Randel 6; OU)
Senecio imparipinnatus Klatt.
S. obovatus Muhl., var. *rotundus* Britt.
S. plattensis Nutt.
Serinia oppositifolia (Raf.) Kuntze
Silphium asperrimum Hook.
S. Gatesii Mohr.
S. laciniatum Torr., var. *Robinsonii* Perry
Solidago altissima L.
S. mollis Bartl.
S. nemoralis Ait., var. *nemoralis*
S. nemoralis Ait., var. *decemflora* (DC.) Fern.
S. rigida L.
S. speciosa Nutt., var. *angustata* T. & G.
S. ulmifolia Muhl.
Sonchus asper (L.) Hill
Taraxacum erythrospermum Andrz.
T. officinale Wiggers, var. *officinale*
Thelesperma intermedium Rydb.
Verbesina encelioides (Cav.) B. & H., var. *encelioides*
V. helianthoides Michx.
Vernonia baldwini Torr., var. *baldwini*
V. baldwini Torr., var. *interior* (Small) Schub.
Xanthium italicum Mor.
X. pensylvanicum Wallr.
Xanthocephalum dracunculoides (DC.) Shinners

SUMMARY

Collections of the vascular flora of Pontotoc County, Oklahoma, were made by employing a combination of intensive and extensive collecting methods. These specimens plus others from the Bebb Herbarium of the University of Oklahoma were examined carefully, identified, and listed. A total of 98 families represented by 380 genera, 698 species and 287 varieties, subspecies and forms, native to, or naturalized in the county, was found. The largest families, with numbers of species in each, were: Compositae 101, Gramineae 82, Leguminosae 59, Cyperaceae 31, Umbelliferae 22, Labiatae 21, Cruciferae 21, and Euphorbiaceae 20. These eight families contain 51 percent of the total flora of the county.

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Distribution of the Tulip Tree (Liriodendron tulipifera L.) in Southwestern New York[1]

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The tulip tree (*Liriodendron tulipifera* L.) is one of the characteristic species abundantly represented in climax communities over a considerable portion of the eastern deciduous forest of the United States. It occurs naturally throughout the eastern and central states, north to Lake Ontario and Grand River, Michigan, and south into northern Florida. It is found in all the states east of the Mississippi River except Maine, New Hampshire, Vermont, and Wisconsin, and west of the Mississippi in parts of Louisiana, Oklahoma, and Missouri (Betts, 1954).

This species has a limited distribution in southwestern New York, which is near the northernmost limit of its range. In Zenkert's (1934) systematic account of the flora of the Niagara Frontier, tulip tree is listed as "rather frequent" and "solitary to sparse." He reported its occurrence in situations similar to those favoring *Magnolia acuminata,* in the lowlands north of the Allegheny Plateau, in rich low woods, and sometimes along the crests of ravines. The vicinity of Dunkirk, New York, was not included in Zenkert's list of locations in which the tulip tree occurs. In June, 1954, a survey of the forests in the Dunkirk region was begun. The purpose of this study was to determine the occurrence of *Liriodendron tulipifera,* its abundance and frequency in communities where it is found, and the composition of these communities. Such data should be helpful in understanding the distribution and behavior of a species growing near the limits of its geographic range.

Study Area

PHYSIOGRAPHIC CONDITIONS

Dunkirk is situated in Chautauqua County and is part of the Niagara Frontier floral region which includes the area within a radius of about 50 miles of Buffalo, N. Y. (Zenkert, 1934). Dunkirk is approximately 43 miles southwest of Buffalo, at latitude 42° 29′ N., longitude 78° 20′ W.

Topographically, four-fifths of Chautauqua County consists of a plateau of moderate altitude, and the remainder is a plain. Many portions of the lake plains have low gradients, smooth surfaces, regular drainage, and fine

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soils (Bowman, 1911). These flats, in sharp contrast to the rough morainic country inland, were once portions of the lake bottom when the continental ice formed the northern border of Lake Erie. The lake plain varies in width from 2 to 5 miles, and ranges in elevation to 300 feet above the level of Lake Erie; the lake is approximately 573 feet above sea level (Fenneman, 1938). The deeply dissected plateau varies in slope from a maximum in the southeastern part where a rise in altitude of 700 feet takes place in about one-and-a-half miles, to a minimum in the northeastern part. The elevation of the plateau is from 1,600 to 2,100 feet above sea level, with the maximum elevation in the southeastern part where the smoothing action of the glaciers was at a minimum (Morrison *et al.*, 1914).

GEOLOGIC HISTORY

A series of events of profound influence on the drainage and topography of this region, as well as on the development of the flora, occurred during the Pleistocene Period. Beginning east of James Bay in Canada, the Labradorean ice sheet invaded nearly all of eastern Canada and a large section of northeastern United States. Owing to the peculiar contour of the ice front the southernmost extremity of the present Niagara Frontier Region was situated at the very edge of the last advance of the glaciers (Zenkert, 1934). Behind the great terminal moraine a number of recessional moraines mark the stations at which the glaciers formed lakes, ponds and shallow basins. The abandoned beaches of some of the smaller lakes are represented today by surface deposits of sand and gravel found at some distance from the present lakes (Bowman, 1911; Fenneman, 1938).

The consolidated rocks of the region consist of beds of nearly horizontal sedimentary rock, elevated as a mass from the sea before the close of Paleozoic times. These sedimentary formations were deposited in the Paleozoic seas which encroached upon the interior of North America through the Cambrian, Ordovician, Silurian, and Devonian periods. During this time southwestern New York was occupied almost continuously by marine waters in which sediments were deposited, consisting of shales, limestones, sandstones, and conglomerates, which were later to form the Allegheny Plateau (Hartnagel, 1940).

SOIL

The Dunkirk region is situated within the major soil province designated by Kellogg (1936) as the gray-brown-podzolic. The soils of the region do not differ much in the source of their parent material, having been derived mainly from sandstones and shales of Devonian age with an addition of igneous and metamorphic rock deposited by the glaciers (Morrison *et al.*, 1914). The humid temperate climate produces leached acid soils. Most of the soils in the plateau portion (somewhat poorly drained) are classified as podzolic and brown podzolic soils; those of the lake plain as gray-brown podzolic. Both of these soil groups are strongly acid to slightly acid. Gray-brown podzolic soils have accumulated some clay in the subsoil at 10 to 15 inches below the surface; podzols and brown podzolic soils have accumulated iron and humus in the subsoil. The nearly level-bedded shale,

siltstone, and fine-grained sandstone bedrock underlying the glaciated land surface must have contained small amounts of lime, since free lime is found in most of the glacial till on the plateau below depths of 3 to 12 feet (Feuer *et al.*, 1955).

Although the soils of southwestern New York have a common source, they differ widely from place to place in the processes by which they were accumulated. On this basis, Finley (1955) in a recent general survey grouped the soils of Chautauqua County into six divisions: 1) glacial, 2) glacioresidual, 3) glacial-lake or mixed glacial-lake and glacial, 4) semi-residual, 5) water-laid, and 6) highly organic soils. The major soil types on the lake plain consist of lake deposits and semi-residual soils. These soils, of medium to heavy texture, are moderately well drained to poorly drained, and are acid to slightly alkaline. Under good land management they produce high yields of grapes, tree fruits, berries, truck and general farm crops. Most of the bottomlands traversing the lake plain are shallow and narrow, coming out of deep gorges along the escarpment. The soils are generally undifferentiated because they are so mixed in drainage, texture, and parent materials (Finley, 1955). In this study the primary interest is in the soils along the northern part of Chautauqua County and the southwestern part of Erie County, at elevations of 800 to 1,000 feet above sea level.

CLIMATIC FEATURES

The Dunkirk region is in the Great Lakes climatic division of New York (Mordoff, 1949). The Great Lakes cause a slight northward bend in the isotherms in October, owing to the retention of the summer heat by the water mass, and the bend becomes more pronounced until January, after which it diminishes. In March the lakes probably cease to act as a source of warmth (Zenkert, 1934). The tempering influence of the lakes is noticeable for a distance of 30 miles inland (Kendrew, 1927). This results in a marked difference between the length of the growing season on the lake plains and in the plateau regions. The length of the growing season on the lake plain averages about 170 days, and in the uplands about 148 days (Morrison *et al.*, 1914).

Dunkirk is situated in the so-called Grape Belt, a strip which extends along the southern shore of Lake Erie for a distance of about 60 miles, and is from 2 to 6 miles wide. Because of the ameliorating influence of the lake, this belt enjoys the most temperate climate in New York State, except for the region along the Atlantic Coast. The tempering influence of the lake holds vegetation in check in the spring until danger from frost is over, and results in long mild autumns with unusually late fall frosts (Kendrew, 1927; Mordoff, 1949).

Climatic data are available for Fredonia, N. Y., 3 miles south of Dunkirk, on the lake plain. The mean annual temperature is 48.6° F; the mean annual temperature for the growing season (May 1 to September 30) is 65.4° F. The average annual temperature for January is 27.6°; for July, 71.3°. The maximum temperature recorded is 98°; the minimum is −26°. The average date of the last killing frost in fall is October 21. The average length of the growing season is 173 days. The mean annual precipitation is 36.72

inches, distributed throughout the year as follows: Jan. 2.40 inches, Feb. 2.04, March 2.42, April 2.73, May 3.26, June 3.49, July 3.16, Aug. 3.20, Sept. 3.78, Oct. 3.91, Nov. 3.33, Dec. 3.00. The mean annual relative humidity is 76 percent; for the frostless period it is 74 percent (Modoff, 1949). The mean annual wind velocity at Buffalo, N. Y., is 14.6 miles per hour; the prevailing direction of the wind is southwest. The wind velocity for the growing season is 12.7 miles per hour (U. S. Weather Bureau, 1953). The Niagara Frontier is in the eastern cloudy belt, and has a mean sunshine for the growing season of approximately 62 percent, the lowest values being recorded in the southern uplands and the highest in the northern lowlands (Mordoff, 1949).

VEGETATION

According to Braun (1950) the Dunkirk region is in the beech-maple association which occupies much of the till plains of Ohio and Indiana, the western end of the glaciated Allegheny Plateau in northern Ohio and western Pennsylvania, and the southern part of the Great Lakes section, almost surrounding Lakes Erie and Ontario. The beech-maple forest was derived from the mixed mesophytic association by postglacial migration, and is the climax stage in its region. The dominants are *Fagus grandifolia* and *Acer saccharum;* the former is the more abundant canopy tree, the latter a codominant in the canopy or a dominant in the understory. Associated most commonly with these are *Tilia americana, Fraxinus americana, Liriodendron tulipifera, Quercus rubra, Quercus alba,* and *Tsuga canadensis.*[2]

The land surrounding the Great Lakes has been available for plant occupancy for only about 20,000 years (Braun, 1950). Some members of the sub-arctic flora found a favorable environment in the southern part of the glaciated region, particularly in the Allegheny uplands. Zenkert (1934) listed at least 15 species of trees and shrubs, and a greater number of herbaceous species of northern origin which may be found in the Niagara Frontier floral region. During the Champlain era, marked by a downward movement of the earth's crust, this region was suitable for the growth of more southerly vegetation. The influence of this era can still be traced north of the Allegheny Ridge, where there is a scarcity of evergreens and the presence of such typically southern species as magnolia, tulip tree, and honey locust (Edson, 1940).

None of the vegetational areas of the country has been more completely altered by man than the vast deciduous forest which formerly occupied the northeastern portion of the United States. The dominant species in this early forest seem to have been *Prunus serotina, Acer saccharum, Tilia americana, Tsuga canadensis, Betula lutea, Fraxinus americana, Castanea dentata, Quercus rubra, Fagus grandifolia* and *Pinus Strobus* (Gordon, 1940; Edson, 1940; Zenkert, 1934). *Liriodendron* seems never to have been a dominant in this forest, though it is sometimes listed as a codominant.

Notable among the factors which destroyed the primeval forest of this region are: frequent and often uncontrolled burning practices of the American Indian; windfalls caused by tornadoes, hurricanes, etc.; the practice of girdling of trees by the Indians and pioneers; and, chiefly, the early lumbering opera-

[2] Nomenclature used throughout this paper follows Fernald (1950).

tions of the white man, with clearing of vast stretches of forest for settlement and agricultural purposes (House, 1927; Gordon and Alexander, 1940). Deforestation has succeeded in transforming this dense forest into a relatively treeless agricultural area.

More than one-half the forest land of southwestern New York today is occupied by the sugar maple-beech type, which occurs principally on the northern slopes and at higher elevations. The aspen type is found in one-fifth of the forest. Sixteen percent is in the ash-elm-maple type commonly found on the moister sites and along stream bottoms. White oak and red oak types occupy 9 percent of the forest land and are generally on the better sites on the south slopes. Softwood types, consisting of white pine and hemlock, account for only one percent of the commercial forest-land area. Only 10 percent of the saw timber stands on commercial forest lands in this region have more than 5,000 board feet per acre (U. S. D. A. Forest Statistics, 1954).

METHODS

After a general survey of the region, communities containing the tulip tree were selected for phytosociological study by means of the quadrat method, following the general procedure described by Oosting and Billings (1939) and Gates (1949). Each stand was sampled by ten 10-m^2 nested quadrats established on alternate sides of compass lines. The distance between quadrats was 10 meters, and between the lines 20 meters. Within these sample areas the tree, shrub, and herbaceous layers were studied. The number of trees of each species was recorded, as well as the diameter at breast height (d.b.h.). In the northwest corner of each major quadrat a 4-by-4 meter square was laid off, within which all species of shrubs and tree transgressives (trees under one inch d.b.h.) were listed. In a one-meter square in the same corner of the major quadrat the herbaceous plants were listed according to species. In each series of ten quadrats there were included 1,000 square meters of the arboreal vegetation, 160 square meters of the shrub and tree transgressive layer, and 10 square meters of the herbaceous layer. Trees encountered in the quadrats were grouped according to their d.b.h. into the following diameter classes: 12 inches or more, 6 to 12 inches, 3 to 6 inches, 1 to 3 inches. Trees under one inch were included with the shrubs. Density and frequency of each species of tree, shrub, and herb were computed. Percentage basal area of each tree species was determined. Tree age was determined with the aid of a Swedish increment borer; height was measured by means of a hypsometer.

RESULTS OF SURVEY

The survey of the Dunkirk region revealed that stands containing the tulip tree are few and widely scattered in this agricultural belt. The tulip tree was found in the following locations within a radius of about 27 miles of Dunkirk, N. Y.: Van Buren, Laona, Silver Creek, Cassadaga, Gowanda, Zoar Valley, Westfield, and Chautauqua Gorge. Some of these locations which exhibited good stands of tulip trees were selected for field studies; others with poor representation of this species were not considerd suitable for quadrat studies. Within immediate confines of Dunkirk practically all forests have been removed. Some tulip trees were found in the moist bottomlands

along the Canadaway Creek. These trees, few in number and widely scattered along the narrow edges of farms and pastures bordering the creek, are the only remains of the vast forest which covered this region a century ago.

At Van Buren, 4 miles west of Dunkirk, one second-growth stand remains in which only 4 mature tulip trees could be located, in association with beech, sugar maple, ash, and some oaks. Young tulip trees are not present, perhaps because of the shade of the rather dense canopy above. On the margins, where competition with other species is at a minimum and light is abundant, a fairly large number of tulip tree seedlings and saplings was discovered.

At Silver Creek, 8 miles east of Dunkirk on Route 20, *Liriodendron* was found on the west slope of the deep ravine south of the town. Several large trees, ranging from 10 to 15 inches d.b.h., were located. A limited number of seedlings occurred in open spaces in direct sunlight. This forest shows no signs of recent influence of man, due no doubt to the difficulty of approach on the steep slope. Remnants of past vegetation litter the ground. Large trees remain where they have fallen, often lying one across another, producing a giant network of rotting vegetation. This condition, together with the dense undergrowth of briars and brambles, makes the hillside almost impenetrable.

At Cassadaga, 10 miles south of Dunkirk, only a few tulip trees were found in the narrow stretches of forest bordering Cassadaga Lake. Tulip trees were also found on the Indian Reservation near Gowanda, about 20 miles southeast of Dunkirk. Extensive lumbering has eliminated most of the larger trees of all species, except in some very dense stands at a considerable distance from the main roads. Some smaller tulip trees with diameters up to 10 inches were found. The presence of large stumps shows that this species was formerly abundant here.

The locations selected for study are the following: Location I—Laona, Location II—Westfield, Location III—Chautauqua Gorge, Location IV—Gowanda, Location V—Zoar Valley.

In the analysis of these locations no attempt has been made at completeness in setting forth the entire floristic composition of the various communities. The primary aim was to note the occurrence and relative abundance of the tulip tree and to indicate some of the more conspicuous features of the habitat in which it occurs, including the tree and shrub associates, and the more common herbaceous species.

DESCRIPTION OF STANDS

Location I (Laona, about 7 miles south of Dunkirk, along Route 60 to Jamestown).—Shumla Road descends from the main highway into a valley which in its lower portion has been cleared and is used for grape growing. On its sharply rising slopes scattered forest areas are found. Canadaway Creek flows along the floor of the valley. Along the beds and sides of this depression may be seen the rock formations of the Portage Shales. Hemlocks grow in profusion in and along the basin of this stream and along its upper waters. The name "Canadaway" was given by the Indians and means "flowing through the hemlocks," indicating the prevalence of this species in former times (Edson, 1940).

From the flat plain at the level of the stream, the sides of the valley rise abruptly, the slope being from 30 to 40 percent. The elevation of this locality is 900 to 940 feet above sea level, and at the top of the slope, 1,000 feet. Topography is rolling or hummocky, and shale outcroppings are present. The soil is moderately well drained to somewhat poorly drained, loose, not heavy in texture, and shows signs of considerable past erosion. The pH ranges from 5.5 to 5.8. The soil is derived from glacial till outwash with some lacustrine influence. There are some colluvial benches, with deposition from above. Seepage areas are present along these slopes.

The forest occupying the hillsides is second growth. Height of the overstory is not more than 50 feet. The number and variety of tree species indicate a transition from an earlier stage to a near-climax stage of succession. Among the sub-climax species are *Salix nigra* and *Robinia pseudo-acacia*, occurring along the creek and lower levels, the latter also at higher levels. *Populus tremuloides*, species of *Pyrus* and *Craetaegus*, and *Prunus pennsylvanica*. *Liriodendron tulipifera* is best represented on the southeast slope.

Twenty 10-m^2 nested quadrats were established on the southeast sloping hill along a line approximately 50 feet above the stream level. Table I shows the average density, frequency and percentage basal area of all the tree species on the basis of ten 10-m^2 quadrats. *Fraxinus americana, Acer*

TABLE I.—Density (D), frequency (F), and percentage basal area (BA) of tree species in the region of Dunkirk, N. Y. Based on sample areas of 1,000 square meters, or ten 10-meter square quadrats in each stand.

	Location I			Location II			Location III		
	D	F	BA	D	F	BA	D	F	BA
Acer rubrum	....	....	.....	22	50	6.5	....	.....	.....
A. saccharum	30	80	12.2	50	80	6.4	32	100	15.3
A. spicatum	....	....	.....	10	60	2.6	....	.....	.....
Betula lenta	2	20	.5	4	20	.2	....	.....	.....
B. lutea	16	40	6.9	10	20	1.4	5	30	3.2
Carpinus caroliniana	21	40	4.6	....	....	.....	8	40	4.0
Carya glabra	3	20	.8	....	....	.....	....	.....	.....
Crataegus sp.	15	40	1.6	20	70	2.2	....	.....	.....
Fagus grandifolia	34	50	11.6	14	40	7.9	25	90	19.4
Fraxinus americana	25	70	21.9	18	90	9.7	12	80	12.0
Liriodendron tulipifera	6	40	5.5	21	90	31.8	32	80	29.8
Magnolia acuminata	....	....	.....	....	....	.....	3	20	.6
Ostrya virginiana	12	40	5.5	8	20	.5	....	.....	.....
Pinus strobus	....	....	.....	4	20	.9	....	.....	.....
Platanus occidentalis	1	10	.3	....	....	.....	2	10	1.6
Populus grandidentata	20	40	3.1	5	30	1.6	....	.....	.....
P. tremuloides	4	20	1.1	4	20	1.3	....	.....	.....
Prunus pennsylvanica	5	20	.7	8	20	1.5	....	.....	.....
P. serotina	....	....	.....	2	20	.4	2	20	1.6
Pyrus sp.	8	30	1.8	17	30	5.1	....	.....	.....
Quercus alba	....	....	.....	....	....	.....	....	.....	.....
Q. rubra	1	10	2.6	4	20	1.4	3	20	1.6
Robinia pseudo-acacia	7	40	10.3	....	....	.....	....	.....	.....
Tilia americana	5	20	5.3	1	10	.3	13	40	7.2
Tsuga canadensis	5	20	2.7	20	40	19.5	9	50	1.4
Ulmus americana	4	20	2.6	4	20	1.3	1	10	.8
U. fulva	....	....	.....	3	20	1.9	....	.....	.....

saccharum, Fagus grandifolia, and *Robinia pseudo-acacia* were found to be the dominant tree species. *Fraxinus americana* had the largest percentage basal area, 21.9, a density of 25 and a frequency of 70 percent; five trees measured above 12 inches d.b.h., with 7 others in the 6-12 inch class. In the transgressive layer *F. americana* had a relatively high density of 30 and a frequency of 80 percent. Though slightly more numerous than *F. americana, Acer saccharum* had a smaller basal area, most of the trees being not more than 3 inches d.b.h. The vigor of this species became apparent in sampling the shrub layer, where 66 transgressives have a frequency of 70 percent were counted. *Fagus grandifolia* had a high density of 34, but trees of this species were rather small, having a basal area of only 11.6. Transgressives were less abundant and less widespread than those of *Acer saccharum. Robinia pseudo-acacia* was represented by 7 large trees which covered 10.3 percent of the total basal area; no transgressives were encountered. It seems likely that the temporary role of *R. pseudo-acacia* in this stand has ended. Other species represented were *Ostrya virginiana, Betula lutea, Prunus pennsylvanica, Tilia americana,* and *Tsuga canadensis* (cf. Table I). *Liriodendron* was generally poorly represented, having a density of 6, a frequency of 40 percent, and a basal area of 5.5. Among the transgressives *Liriodendron* was somewhat more abundant, its density being 26 and its frequency 40 percent.

The shrub stratum was dominated by *Hamamelis virginiana* and *Viburnum acerifolium,* having high densities of 34 and 40 respectively (Table II).

TABLE I.—(*continued*)

	Location IV			Location V		
	D	F	BA	D	F	BA
Acer rubrum	....	....	.....	....	....	.....
A. saccharum	49	70	22.2	35	80	7.2
A. spicatum	....	....	.....	....	....	.....
Betula lenta	....	....	.....	5	20	1.1
B. lutea	....	....	.....	10	20	4.5
Carpinus caroliniana	27	50	2.8	9	40	1.6
Carya glabra	3	20	1.6	....	....	.....
Crataegus sp.	....	....	.....	40	60	10.8
Fagus grandifolia	70	90	16.3	2	10	.1
Fraxinus americana	17	50	9.9	19	80	5.5
Liriodendron tulipifera	18	40	13.0	76	80	43.5
Magnolia acuminata	3	20	1.6	....	....	.....
Ostrya virginiana	....	....	.....	....	....	.....
Pinus strobus	1	10	.3	....	....	.....
Platanus occidentalis	....	....	.....	....	....	.....
Populus grandidentata	3	20	3.1	....	....	.....
P. tremuloides	....	....	.....	....	....	.....
Prunus pennsylvanica	....	....	.....	....	....	.....
P. serotina	....	....	.....	....	....	.....
Pyrus sp.	1	10	.3	41	60	7.8
Quercus alba	2	20	1.3	....	....	.....
Q. rubra	7	30	8.0	2	10	.6
Robinia pseudo-acacia	....	....	.....	....	....	.....
Tilia americana	12	40	6.5	....	....	.....
Tsuga canadensis	7	40	2.6	42	40	15.3
Ulmus americana	11	30	6.9	....	....	.....
U. fulva	5	20	4.5	5	20	.8

Cornus rugosa and *Lindera benzoin* were fairly abundant. In the herbaceous layer *Achillea millefolium, Maianthemum canadense, Thalictrum polygamum,* and *Podophyllum peltatum* were represented (Table III) *Dryopteris marginalis* occurred near the wet seepage areas. *Solidago canadensis* was found in open spaces between some of the trees. Scattered clumps of *Vinca minor,* probably escaped from cultivation, were observed.

The presence of the tulip tree on this site may be explained by the fact that this forest was cleared in recent times, either by lumbering or fire, or possibly both. The large number of sub-climax species indicates a struggle for dominance among the many invading species. In the open canopy the mature tulip tree is able to compete successfully for a place in the community.

TABLE II.—Density (D) and frequency (F) of shrubs, vines and tree transgressives in the region of Dunkirk, N. Y. Based on sample areas of 160 square meters, or ten 4-meter square quadrats in each stand.

	I		II		III		IV		V	
	D	F	D	F	D	F	D	F	D	F
Acer rubrum	....	....	19	30	....	....	....	....	4	20
A. saccharum	66	70	75	90	21	50	15	60	88	90
A. spicatum	2	10	....	....	....	....	30	50	....	....
Amelanchier canadensis	....	....	4	30	....	....	....	....	....	....
Betula lutea	....	....	....	....	1	10	....	....	....	....
Campsis radicans	....	....	8	20	....	....	....	....	....	....
Carpinus caroliniana	3	10	....	....	....	....	....	....	8	30
Carya glabra	3	20	....	....	....	....	28	30	....	....
Castanea dentata	....	....	8	30	13	30	10	40	....	....
Convolvulus sepium	....	....	4	10	....	....	....	....	4	20
Cornus rugosa	11	40	9	20	....	....	....	....	2	20
Crataegus sp.	2	10	10	40	....	....	....	....	....	....
Fagus grandifolia	21	50	15	40	31	90	35	70	....	....
Fraxinus americana	30	70	33	100	16	70	....	....	38	90
Hamamelis virginiana	34	40	....	....	14	50	24	50	65	70
Lindera benzoin	9	30	....	....	3	20	4	20	....	....
Liriodendron tulipifera	26	40	14	50	24	60	6	30	16	50
Magnolia acuminata	1	10	3	20	....	....	....	....	1	10
Ostrya virginiana	....	....	13	40	....	....	....	....	....	....
Parthenocissus quinquefolia	....	....	....	....	....	....	12	30	10	40
Pinus strobus	....	....	5	40	....	....	2	20	....	....
Populus grandidentata	2	10	....	....	....	....	....	....	....	....
P. tremuloides	....	....	6	30	....	....	....	....	....	....
Prunus pennsylvanica	2	10	....	....	....	....	....	....	4	20
Quercus rubra	3	20	24	60	13	50	18	50	....	....
Rhus radicans	8	30	....	....	....	....	5	20	17	30
R. typhina	2	10	....	....	....	....	....	....	4	20
Rubus sp.	....	....	....	....	5	20	....	....	....	....
Smilax herbacea	3	20	....	....	2	10	....	....	....	....
S. rotundifolia	....	....	3	20	....	....	....	....	....	....
Tilia americana	5	30	2	20	5	20	....	....	....	....
Tsuga canadensis	....	....	....	....	9	50	14	40	3	30
Ulmus americana	....	....	....	....	3	30	....	....	....	....
U. fulva	....	....	1	10	....	....	....	....	....	....
Viburnum acerifolium	40	50	7	30	....	....	10	20	....	....
V. alnifolium	....	....	....	....	....	....	....	....	2	10
Vitis aestivalis	3	20	5	30	....	....	7	20	5	30
V. labrusca	8	40	6	40	....	....	....	....	4	20

The thinness of the canopy of the dominant trees provides tulip tree seedlings with ample light for development. Also favorable to this species are the moderate local climatic conditions. The sloping hills protect this stand from drying winds, while the topography permits full exposure to sunlight. In addition, the proximity of Lake Erie, with its moderating temperature influence, makes the protected valley warmer and less variable than adjacent regions. Canadaway Creek, flowing along the floor of the valley, as well as the seepage springs on the slope, provide a moist atmosphere favorable to the tulip tree. It is significant that the tulip tree does not occur in the very wet seepage areas, nor in dry eroded areas, but only on deep and well-drained soils.

Considering the relative abundance of tulip tree seedlings in this stand, it should normally be expected that in time this species will become an important member of the ash-sugar maple-beech community. Although topographic and climatic conditions are favorable, however, it is possible that, as the large number of maple and ash seedlings develop, competition for light will be too severe for the shade-intolerant tulip tree, thus limiting the development of the species.

Location II (Westfield, about 20 miles west of Dunkirk, near the Westfield waterworks).—From the waterworks a narrow dirt road runs south, ascending gradually as it approaches the Allegheny Ridge. At 1.3 miles from the waterworks the east side of the road falls away sharply in a steep undulating slope. For a short distance the slope varies from 20 to 25 percent, then drops sharply towards Cattaraugus Creek which runs along the foot of the hill. The elevation of this location is approximately 940 feet above sea level. The soil is principally made up of fine sand, gravel, and some shale fragments. It is moderately well drained and slightly acid, the pH ranging from 5.6 to 6.2. Slight to moderate erosion is taking place. The soil is alluvial outwash, derived from a glacial till mix. The A-layer is about 6 inches thick, the B-layer reaches to a depth of about 36 inches, and the C-layer of parent material of glacial till or outwash gravel extends approximately 10 to 15 feet to the shale rock. The topsoil is gray-brown, light-textured, and contains considerable organic matter; the subsoil is yellowish-brown, friable, and loose.

On this rolling slope a well-developed forest once flourished. Heavy cutting or fire has stripped the forest of large trees. The second growth vegetation has not reached maturity, and appears to be in one of the last of the transitional stages before the climax. A dense mat of decaying vegetation covers the moist forest floor. The well-spaced trees form a closed canopy. No clearly marked shrub layer is apparent.

Thirty 10-m^2 quadrant sample plots were laid along a line paralleling the road at a distance of approximately 300 feet. For purposes of comparison of this stand with the others discussed in this report the total density, frequency, and basal area of all species were averaged on the basis of ten 10-m^2 quadrats. *Liriodendron tulipifera* was the tallest tree in this stand and was the chief dominant species. Its density was 21, frequency 90 percent, and basal area 31.8. Five trees measured more than 12 inches d.b.h.; the remainder varied between 6-12 inches. In the transgressive layer thirteen seedlings were counted, with a frequency of 50 percent. *Tsuga canadensis* was the codominant, having a basal area of 19.5, a density of 20, and a frequency of 40 percent;

TABLE III.—Density (D) and frequency (F) of herbaceous species in the region of Dunkirk, N. Y. Based on samples of 10 square meters, or ten 1-meter square quadrats in each stand.

	I		II		III		IV		V	
	D	F	D	F	D	F	D	F	D	F
Achillea millefolium	5	20	3	10	14	30	8	30	....	....
Adiantum pedatum	....	....	....	....	3	10	....	....	13	30
Agrimonia gryposepala	....	....	....	....	....	....	2	10	....	....
Anemone virginiana	2	10	5	20	22	50	....	....	3	10
Arctium Lappa	....	....	....	....	....	....	5	10	....	....
Arisaema triphyllum	4	20	7	20	2	10	....	....	7	20
Asarum canadense	....	....	....	....	....	....	6	10	8	30
Aspidium spinulosum	....	....	....	....	....	....	....	....	2	10
Aster spp.	11	40	5	20	13	30	29	70	12	30
Athyrium Felix-femina	....	....	....	....	2	10	....	....	....	....
Bidens cernua	2	10	....	....	....	....	....	....	1	10
Botrychium virginianum	....	....	....	....	....	....	....	....	3	10
Carex spp.	2	10	....	....	7	20	....	....	4	10
Caulophyllum thalictroides	....	....	2	10	....	....	3	20	....	....
Chimaphila maculata	....	....	....	....	....	....	5	20	10	20
Chrysanthemum spp.	7	20	5	10	....	....	....	....	3	10
Cirsium vulgare	1	10	....	....	....	....	5	20	....	....
Collinsonia canadensis	....	....	7	40	5	20	3	10	....	....
Dioscorea quartenata	....	....	3	20	....	....	....	....	....	....
Dryopteris marginalis	4	20	8	30	....	....	....	....	....	....
D. noveboracensis	....	....	....	....	....	....	....	....	2	10
Equisetum arvense	4	20	....	....	18	40	....	....	....	....
E. hyemale	....	....	....	....	17	30	....	....	....	....
Fragaria virginiana	....	....	....	....	35	30	47	60	....	....
Galium triflorum	5	10	10	20	....	....	....	....	4	10
Geranium maculatum	2	10	....	....	....	....	....	....	....	....
Geum canadense	....	....	2	10	....	....	3	10	....	....
Hepatica triloba	13	30	....	....	7	20	....	....	....	....
Hypericum perforatum	3	10	....	....	5	20	....	....	1	10
Impatiens biflora	....	....	....	....	....	....	....	....	2	10
Lycopodium complanatum	....	....	20	60	....	....	....	....	....	....
L. lucidulum	....	....	....	....	....	....	6	20	3	10
L. obscurum	....	....	15	20	20	20	....	....	7	20
Maianthemum canadense	7	20	16	30	....	....	4	10	....	....
Medeola virginiana	....	....	....	....	....	....	....	....	3	20
Mitchella repens	....	....	....	....	10	30	....	....	4	10
Onoclea sensibilis	....	....	12	20	....	....	....	....	....	....
Osmunda cinnamomea	3	10	....	....	....	....	....	....	....	....
Oxalis acetosella	....	....	....	....	30	20	....	....	12	20
Plantago lanceolata	2	10	....	....	....	....	3	10	....	....
Podophyllum peltatum	6	30	10	30	8	40	6	20	15	40
Polysticum acrosticoides	....	....	12	20	7	30	....	....	6	20
Potentilla canadensis	4	10	....	....	....	....	37	40	....	....
Prunella vulgaris	....	....	....	....	12	30	....	....	....	....
Pteridium aquilinum	....	....	....	....	3	20	2	10	3	20
Rumex Acetosella	....	....	....	....	....	....	7	20	....	....
Smilacina racemosa	5	10	....	....	....	....	3	20	5	20
Solidago canadensis	15	50	8	30	31	60	7	20	9	30
S. patula	....	....	....	....	....	....	10	30	....	....
Thalictrum dioicum	....	....	6	30	....	....	....	....	....	....
T. polygamum	9	50	7	20	....	....	....	....	4	20
Vinca minor	10	20	17	40	25	40	15	20	7	20
Viola sp.	....	....	7	10	....	....	....	....	....	....

no transgressives were included in the sample area, though some were observed outside the quadrat area. *Acer saccharum* was more than twice as abundant as *Liriodendron tulipifera*, with a density of 50, and a frequency of 80 percent. Its basal area, however, was only 6.4 percent, since most of the trees were under 3 inches d.b.h. Among the transgressives this species had an unusually high density of 75 and a high frequency of 90 percent. *Fraxinus americana* and *Fagus grandifolia* had a basal area of 7.9 and 9.7 respectively. The former was abundant in the transgressive layer (cf. Table II).

Prunus pennsylvanica was formerly an important member of this community, but now is dying out. Only 8 living trees were found, but large numbers of dead trees 4-8 inches d.b.h. were observed. No seedlings were found. *Castanea dentata* was also abundant in the past. Several diseased trees were still standing, the largest measuring twenty-two inches d.b.h. Considerable numbers of chestnut saplings were encountered, some as much as 10 feet in height. *Acer rubrum*, *Pyrus* spp. and *Populus grandidentata* constituted a large percentage of the remaining trees (cf. Tables I and II).

The shrub stratum was not clearly marked, and was dominated chiefly by tree seedlings. *Viburnum acerifolium* and *Cornus rugosa* were the most common shrubs. Among the vines were *Vitis aestivalis*, *V. labrusca*, and *Campsis radicans*. *Rhus radicans*, so abundant in some of the other locations, was absent in this stand. Comprising a large percentage of the herbaceous vegetation were *Podophyllum peltatum*, *Vinca minor*, *Dryopteris marginalis*, *Thalictrum polygamum*, and *Lycopodium complanatum*. *Maianthemum canadense* was particularly abundant. *Lycopodium complanatum* and *Onoclea sensibilis* were represented only in this stand (cf. Table III).

The tulip tree is not a recent invader in this stand; in the past it probably occurred with the chestnut. Many large tulip tree stumps were seen, some of these with 12 feet of sprout growth. Increment borings were made on selected living trees and stumps of this species in order to obtain some indication of their age and growth rate. This information obtained is here listed:

Increment borings	Diameter (inches)	Annual Rings
Dead stump	16.0	35
Dead stump	21.0	45
Stump with sprout growth	17.0	44
Living tree in dense stand	8.6	35
Living tree in open stand	8.0	19

The relatively large size of the tulip trees, the vigorous sprout growth of old stumps, and the number of seedlings present, seem to indicate that here is an ideal environment for this species. However, the present dominance of the tulip tree may be only temporary. Most of the tulip trees are large, and although the seedlings are relatively abundant, their number cannot compare with the high density of sugar maple seedlings which dominate the shrub layer. The shade-tolerant sugar maple offers severe competition to the tulip tree and may in time crowd out this light-demanding species. It will be

of interest to note the future development of this forest and to see if the tulip tree can survive in its struggle for light.

Location III (Chautauqua Gorge, 3 miles south of Westfield, on Route 17).—Chautauqua Gorge is a deep ravine paralleling the old Portage Road between Westfield and Mayville. It is a place of unusual scenic beauty. Hartnagel (1940) cited this location as one of the more striking topographic features of southwestern New York. The gorge is a post-glacial formation hollowed out of the soft Devonian shales by small streams which had their source in the morainic uplands along the edge of the Allegheny Plateau. This is the region of the terminal moraine and has a considerable deposit of well-drained glacial till which imparts a hummocky or rolling topography. Chautauqua Creek traverses the deeply carved ravine.

Along the western side of the stream a steep wall or "slip" ascends. This wall has been exposed by a slippage of topsoil, caused by the undermining current of the stream and underground seepage from the precipitous slope. On the slope distinct stratification can be observed, the finer, less erodable sandstone material protruding from the Devonian mud-shale in layers at successive elevations. Upland topography adjacent to the gorge has a slope of 8 to 15 percent, while the gorge itself has an average of 45 to 60 percent. Chautauqua Gorge is between 860 and 900 feet above sea level; the elevation of the ridge at the edge of the gorge is 1,300 feet above sea level.

Soils, derived from acid glacial till, have been deposited by slippage along the precipitous slope. These alluvial soils at the bottom of the gorge extend a short way up the colluvial slopes. The soils are deep, sandy, moderately well drained, and have a pH of 5.6 to neutral. The upper rolling part of the terrain contains glacial soils; the lower part is a mixture of undifferentiated alluvial and colluvial soils.

Arboreal vegetation is found on the steep hillsides of the gorge where deposits of soil have not been carried down through extreme erosion. Large hemlocks abound on the western cliffs. Along the eastern side of the creek the flat plain is from one hundred to several hundred feet in width. On this well-drained bottomland plain a mature forest flourishes, and extends upwards to cover the hillside. The forest vegetation may best be described as luxuriant, with its rich variety of trees, shrubs, and herbs. Trees are large and well spaced, the canopy is close, and the forest floor relatively clear of brush. Total height of the overstory is 90 to 100 feet. The understory is low, varying from 15 to 25 feet. Dominant tree species are *Liriodendron tulipifera, Fagus grandifolia,* and *Acer saccharum. Fraxinus americana* and *Tilia americana* are codominants.

In this tulip tree-beech-sugar maple stand ten 10-m^2 quadrats were established in a line paralleling the creek, approximately 50 feet from the water's edge. The dominant tulip tree had a density of 32, a frequency of 80 percent, and a basal area of 29.8. Most of the trees were large, ten measuring more than 12 inches d.b.h., and twelve measuring 6-12 inches. The largest tree in the sample area was 25 inches d.b.h. Analysis of the shrub layer indicates that conditions are suitable for the reproduction of the tulip tree. Twenty-four transgressives were counted; their frequency was 60 percent.

Fagus grandifolia manifested an unusual degree of development in this

stand, though some of the larger trees were of poor quality. Its density was 25, frequency 90 percent, and basal area 19.4. Seven trees were more than 12 inches d.b.h. One giant beech, not included in the quadrat area, measured 37 inches in diameter. In the shrub stratum *F. grandifolia* had the highest number of transgressives. Thirty-one seedlings were counted; their frequency was 90 percent.

Acer saccharum had a density of 32, the same as for *Liriodendron tulipifera*, but its frequency of 100 percent was higher. The majority of trees was less than 6 inches in diameter, having a total basal area of 15.3 percent, almost half that of *L. tulipifera*. In the shrub stratum twenty-one seedlings were listed. *Fagus americana* and *Tilia americana* were codominants, the former having a density of 12, a frequency of 80 percent, and a basal area of 12 percent; the latter showed poorer development, with a density of 13, a frequency of 40 percent, and a basal area of 7.2. *Carpinus caroliniana, Carya glabra, Tsuga canadensis, Quercus rubra, Prunus serotina* and other tree species were represented (cf. Table I). *Castanea dentata* was formerly abundant here; several dead trees, ranging in diameter from 10 to 15 inches, were still standing. A relatively large number of living chestnut sprouts was observed.

The shrub stratum was composed principally of tree transgressives. *Hamamelis virginiana* was the dominant shrub, having a density of 14 and a frequency of 50 percent. *Lindera benzoin* and *Rubus* spp. were scattered and few. There were no representatives of *Rhus radicans* or *Vitis* spp. The ground stratum was characterized by a great number and variety of herbaceous plants. Practically every species encountered in the other locations could be found here, though all were not sampled in the quadrats. *Anemone virginiana, Fragaria virginiana,* and *Oxalis acetosella* were widely distributed. *Lycopodium obscurum,* not abundant in any of the other stands, was unusually so here. *Equisetum arvense* and *E. hyemale,* had high frequencies of 40 and 30 percent respectively, the latter being found only at this location (cf. Table III).

This stand is still in a state of flux and has not reached maximum development. It may become an excellent example of the beech-sugar maple climax forest. At the present time the tulip tree holds dominance, but it is questionable if this dominance will be permanent as it enters into competition with beech, sugar maple, ash, and basswood. The stand has been heavily lumbered in the past. In the clearings left in the forest it was easy for the tulip tree to become established. Environmental conditions favored its growth in this fertile bottomland plain where the steep hillsides afford protection from drying winds and a warm, moist atmosphere is provided by nearby Lake Erie and Chautauqua Creek. Left to itself, the tulip tree should continue to thrive here. But these ideal conditions also favor other species, and time alone can tell what dynamic changes will take place in the forest composition, whether the tulip tree will be reduced to a codominant in a beech-sugar maple stand, or whether it will be able to maintain its place at all.

Location IV (Gowanda, 20 miles southeast of Dunkirk, at the western extremity of Erie County).—A large-pole sub-saw timber forest (trees generally 8-10 inches d.b.h.) is found on the Zoar Valley Road, 4 miles from the center of Gowanda. On the south-facing slope tulip tree is conspicuously

represented among large beeches and white pines. General topography is undulating to hummocky, with an 8 to 15 percent slope. Elevation ranges between 900 and 940 feet. The gray-brown podzolic soil derived from heavy glacial till, is moderately well drained, of uniform color, and shows little mottling even in the B-layer. The topsoil is a yellowish-brown silt loam, finely textured and of porous structure; subsoil is compact, hard in places, friable under pressure, and contains fine sandy material. Soil pH ranges from 5.6 to 5.8.

Several hundred feet to the south of the road the forest gives way to a marshy area bordering Cattaraugus Creek. Several species of ferns, cattails, and water lilies abound on this moist site. The forest floor lacks dense underbrush and the trees are well-spaced, with a close canopy above. Recent lumbering has removed many of the larger trees. The entire area was cleared approximately 40 years ago. Stumps of aged trees measuring up to 25 inches in diameter show that this was once a mature forest. Average height of the overstory is 65 to 70 feet; one large tulip tree measures 75 feet in height. Beneath the dominant trees there is no clearly defined understory, only a low shrub layer.

Ten 10-m^2 quadrats were laid along the south slope approximately 100 feet from the road. In this 1,000 square meter sample area *Fagus grandifolia* was found to be the dominant species with a density of 70, a frequency of 90 percent, and a basal area of 16.3. Seedlings of this species also dominated the shrub layer. The codominant, *Acer saccharum*, was less abundant, but showed better development, with a basal area of 22.2 percent; few transgressives were found. *Liriodendron tulipifera* numbered 18 mature trees. These had a frequency of 40 percent and a relatively high basal area of 13.0. Only one of these measured more than 12 inches d.b.h.; nine were between 6-12 inches. Among the transgressives only 6 tulip tree seedlings were found, indicating a low rate of reproduction. *Fraxinus americana* was represented by 17 trees, with a frequency of 50 percent, and a basal area of 9.9 percent. Many white ash trees between 6-8 inches d.b.h. were dead or in a diseased condition. *Carpinus caroliniana, Quercus rubra, Tilia americana, Tsuga canadensis, Ulmus americana,* and *U. fulva* were also important members of this community (cf. Tables I and II). *Prunus serotina, Amelanchier canadensis,* and *Populus tremuloides* were abundant, but did not occur within the quadrat area. A large number of chestnut stumps were seen, and 10 chestnut sprouts of vigorous growth were numbered in the shrub layer.

Most abundant of the shrubs were *Hamamelis virginiana* and *Viburnum acerifolium*. The vines, *Parthenocissus quinquefolia, Rhus radicans* and *Vitis aestivalis* were present. *Podophyllum peltatum, Vinca minor, Aster* spp., *Fragaria virginiana,* and *Potentilla canadensis* formed a major part of the herbaceous layer (cf. Table III).

The explanation for the presence of *Liriodendron tulipifera* in this beech-sugar maple-tulip tree stand is the same as that given for its presence in the locations previously described. This stand is somewhat similar to that of Westfield. Recent clearing operations, the gently rolling upland topography, and the moderate local climate influenced by the warm moist winds of Lake Erie and the moisture of Cattaraugus Creek have permitted the species to thrive. Past management of the stand has favored the tulip tree, but it is

doubtful if it is any more than temporary in succession. The quadrat studies have shown that whereas the mature trees were somewhat abundant (18), only six seedlings were counted. It is not likely that the tulip tree will be able to compete for long with the hardy beech and sugar maple seedlings which are found in considerable abundance. Left to itself, this forest should become in time a beech-sugar maple climax type, with little or no representation of the tulip tree.

Location V (Zoar Valley, on the Zoar Valley Road, 8 miles east of Gowanda and one mile east of the Zoar Valley Bridge).—This location, like the preceding one, is situated at the western extremity of Erie County, at an elevation of 960 to 1,000 feet above sea level. An exceptionally fine stand of tulip trees occurs on the south-facing slope, about 300 yards from the road, along the upland break of Cattaraugus Creek. Topography is hummocky and rolling, with a 20 to 30 percent slope. The soil is loose and is moderately well drained to poorly drained in sections. Subsoil is sandy and compact. Wet areas formed through seepage from underground springs are found in which the soil is a dark ooze; subsoil in these areas is heavily mottled, indicating poor drainage. No trees occur on these excessively wet areas. The gray-brown podzolic soil is similar to the soil at the Gowanda location, being derived from glacial till and upland outwash with underlying shale rock. Glacial boulders are scattered on the surface. The pH ranges from 5.6 to 6.0.

The steep colluvial slope is covered by a young, second-growth forest. A dense growth of sumacs, goldenrods, asters, wild raspberries, and Queen Ann's lace lines the margin of the forest facing the road. Further in, mingled with some sumacs, are large numbers of seedlings of tulip tree, beech, sugar maple, and white ash, which are invading the old-field site from above. As the hillside ascends more sharply the sumacs are shaded out by the arboreal vegetation, and the seedlings are replaced by mature trees.

Height of the canopy is about 50 feet; in the lower portions of the slope the canopy is generally open in structure, permitting considerable light to reach the rich and varied herbaceous cover of the forest floor. The stand shows signs of lumbering in recent times, perhaps not more than 15 years ago.

On analysis of a ten 10-m^2 quadrat sample area on the sloping hillside, *Liriodendron tulipifera* was found to be dominant. Seventy-six mature trees were counted; they displayed a high frequency of 80 percent and a total basal area of 43.5 percent. None was over 12 inches d.b.h.; twenty-six measured between 6-12 inches, the remainder less than 6 inches. In the transgressive layer sixteen seedlings were counted; their frequency was 50 percent. Species of *Pyrus and Crataegus* were in great abundance. Most of these were dead or dying, as in the preceding stands, and no seedlings of either species were seen. It seems that they will soon disappear completely. *Tsuga canadensis* and *Acer saccharum* were in considerable abundance, with densities of 42 and 35 respectively. *Fraxinus americana, Carpinus caroliniana,* and *Betula lutea* were important constituents of the stand (cf. Tables I and II). *Acer saccharum* and *Fraxinus americana* were dominant among the transgressives. *Hamamelis virginiana* was the only shrub occurring in the sample area. In the herbaceous layer *Adiantum pedatum, Asarum canadense, Aster*

sp., *Chimaphila maculata*, *Oxalis acetosella*, and *Podophyllum peltatum* were abundant (cf. Table III).

This is probably the best stand of *Liriodendron* in the Dunkirk region. Its high density on this site is unusual, considering the composition of the adjacent forest, and can best be explained by the combination of favorable topography and climate. The abundance of *Crataegus* and *Pyrus* species indicates that the land was formerly open pasture, an area into which the tulip tree could easily invade. The warm south-facing slope overlooking Cattaraugus Creek is climatically ideal for this typically southern species. The sloping sides of the fertile Zoar Valley provide protection from drying winds, and the valley itself acts as a sort of flue through which the warm winds of Lake Erie flow southward.

It is significant that the tulip tree is confined to the lower parts of the slope, and does not occur above approximately 70 feet from the creek level. This proximity to the warm valley bottom and to the water seems definitely related to the occurrence of the species in such abundance. Tulip tree seedlings are invading downwards into the old-field site, but not upwards, where the higher elevation seems unfavorable. Because of this downward invasion, the future of the species in this stand seems assured. Yet, the beech, sugar maple, white ash, and hemlock trees which cover the higher reaches of the slope are also invading downwards, indicating considerable competition for the tulip tree seedlings. It seems probable that, with occasional clearing, the tulip tree should remain the dominant in this stand for many years to come.

DISCUSSION

The occurrence of the tulip tree in the region of Dunkirk, N. Y. is of particular ecological interest. Essentially a southern species, its presence so far north may be explained by the geological history of this region, when, following the Ice Ages, the warmer climate of the Champlain era favored southern species. Present distribution of the tulip tree is comparable to a hand, the palm representing its natural range in the southeastern States, the outstretched fingers those extensions northward where southerly conditions are somehow continued. Thus, along waterways, in sheltered cove situations, and in warm moist valleys the tulip tree is able to thrive in the north. In the region of Dunkirk the species has a discontinuous distribution, occurring in widely separated and scattered patches. Correlation of the general characteristics of the five stands studied is here attempted in order to explain the occurence of the species. These characteristics are chiefly topography, habitat, soil, climate, and plant associations.

Topography.—The five stands discussed in this paper were selected after a general survey of the region. After the conclusion of the field studies the remarkable similarity of each of the stands was noted. All are at approximately the same elevation, the lowest being Chautauqua Gorge, about 840 feet, the highest, Zoar Valley, at 960 to 1,000 feet above sea level. As the Allegheny Plateau is approached, at approximately 1,500 feet above sea level, the tulip tree becomes scarce. All the stands are on south- or west-facing slopes. Particularly significant is the fact that in early spring the snow on the slopes on which the tulip tree occurred had thawed rapidly, while adjacent slopes were still heavily snow-covered.

Steepness of slope is also a noteworthy factor in the occurrence of this species. The tulip tree seems to prefer a gently rolling or hummocky topography, and avoids precipitous slopes. The steepest slope (30 to 40 percent) on which the species occurs is at Laona. The other locations vary from 8 to 30 percent. At Chautauqua Gorge the tulip tree, abundant on the moist bottomland, is not found on the steep slopes adjacent to the bottomland plain.

Habitat.—All five locations are similar in being cove or cove-like situations where the sloping sides of valleys protect from drying winds. Topography in every case is favorable because of the warming sunlight. Two main types of habitat distinguished are 1) moist bottomland, as at Chautauqua Gorge along Chautauqua Creek, and 2) moderately sloping hillsides adjacent to flowing streams, as at Westfield, Laona, Gowanda, and Zoar Valley. Ample moisture is a factor common to each. On steep slopes, as at Laona and Zoar Valley, the tulip tree is limited to elevations 60 or 70 feet above the surface of the flowing water, and avoids the higher reaches of the hillsides and the ridges. This may indicate a dependence of the tree on the moist air proximate to the water bodies.

Soil.—In each of the stands the soil is of the same parent material, being largely glacial till deposits. The pH of the soil in all sites is on the acid side, varying from 5.5 to 6.2, except at Chautauqua Gorge where some horizons are neutral. In every case the soil is loose, moist, of moderately good drainage and of fairly fine texture. The species avoids very wet areas, such as the seepage areas at Laona and Zoar Valley, and dry eroded areas. An abundance of litter and herbaceous cover seems to favor the species.

McCarthy (1933) concluded that the influence of chemical composition of soil on the growth of the tulip tree is apparently slight, and that the tree thrives on soils of many kinds of chemical composition and physical texture, provided these are moist with good drainage. Soil conditions of each of the five stands do not differ significantly from other stands in the same region in which the tulip tree does not occur. It seems, therefore, that the presence of the tulip tree cannot be explained by any local specific physical or chemical properties of the soil.

Climate.—Each of the stands has local climatic features which are particularly suited to the warmth- and moisture-loving tulip tree. All are proximate to Lake Erie and receive its moderating temperature influence. The lake plain has a warmer annual temperature and a considerably longer growing season than the adjacent upland plateau (170 days on the lake plain, 148 days on the uplands—Morrison, *et al.*, 1914). Dissecting the lake plain and extending into the foothills of the Allegheny are deep ravines or gorges through which numerous small tributaries drain into the lake. Each of the stands which best favored the growth of the tulip tree is situated in one of these depressions. These depressions act as channels or flues through which warm air currents from the lake flow southward. In these the mild climatic features of the lake plain are extended for several miles into the upland topography. At higher altitudes and beyond the foothills of the Allegheny the warming influence of the lake dwindles and the tulip tree is not found.

This seemingly slight modification of temperature, as well as the humidity from local streams, is probably a very significant factor in accounting for the presence of the tulip tree in these stands. Microclimatic studies could profitably be made to determine how far south the climatic features of the lake plain are extended in these depressions.[3]

Plant associations.—The chief species of trees associated in the five stands with the tulip tree are, in order of importance, *Acer saccharum, Fagus grandifolia, Fraxinus americana, Betula lutea, Tsuga canadensis,* and *Quercus rubra.* The density and frequency of these species vary considerably from stand to stand and apparently show no relationship to the density and frequency of *Liriodendron tulipifera.* From the large number of chestnut stumps and sprouts in the various locations it may be concluded that the tulip tree thrives in approximately the same habitat which formerly favored *Castanea dentata,* and that it is replacing this species in the forest community.

Of the shrubs, the most significant associated species is *Hamamelis virginiana,* which occurs on cool, moist sites. Whereas some herbs, such as *Podophyllum peltatum, Vinca minor, Arisaema triphyllum,* and *Achillea millefolium,* are conspicuously present in each stand, these species are also abundant in stands lacking the tulip tree, and no particular relationship was noted. Plant associations were not considered significant in explaining the presence of the tulip tree.

As to the future of the tulip tree in the Dunkirk region of southwestern New York, the species seems definitely to be decreasing in woodlands. As the canopy closes off more light, and shade-tolerant species, such as beech and sugar maple, enter into competition, most of the tulip tree seedlings now present will probably be prevented from reaching maturity. On the margins of forests, in open field sites, and in young stands where competition is slight, and light and moisture adequate, the species is definitely increasing. With selective management the tulip tree could be made to spread and develop in suitable areas. Left to itself, and subjected to the natural processes of plant succession, it seems doubtful that the tulip tree will maintain itself in the mature climax forest.

SUMMARY

A phytosociological study of representative forest stands was made in a region within a 27-mile radius of Dunkirk in southwestern New York to determine the occurrence and frequency of *Liriodendron tulipifera,* as well as the composition of the forests in which it occurs. Quantitative data were secured by means of standard quadrat sampling methods. Density and frequency of trees, shrubs, and herbs, and percentage basal area of trees were determined.

The chief associates of the tulip tree in these stands are *Acer saccharum, Fagus grandifolia, Fraxinus americana, Betula lutea, Tsuga canadensis,* and *Quercus rubra.* The density and frequency of these species vary consider-

[3] Further studies should be made on the microclimatic features of each stand to show by quantitative data a possible correlation with the presence of the tulip tree. Also, further investigation of extremely local variations in the texture and drainage of the soils will undoubtedly assist in explaining the distribution of this species.

ably from stand to stand, and apparently show no relationship to the density and frequency of the tulip tree.

The five stands in which the tulip tree is well represented range from 840 to 1,000 feet above sea level. Above 1,500 feet, on the Allegheny Plateau, the species was not found. All the stands are on south- or west-facing slopes above flowing streams. The tulip tree seems to prefer gently rolling or hummocky topography, and avoids precipitous slopes. Best sites are on moderately well-drained soils having an abundance of organic cover.

Neither plant associations nor soil conditions appear adequate to explain the presence of the tulip tree. Local climatic conditions seem to be the chief factor in explaining the discontinuous distribution of this species in widely scattered areas. Each of the stands is situated in a type of valley bordering a stream which drains into Lake Erie. These depressions act as channels or flues through which warm moist air currents from the lake flow southward. The resulting slight modifications of local climate are probably sufficient to account for the presence of the tulip tree in these locations.

The tulip tree thrives in the same general habitat which formerly favored *Castanea dentata* in this region, and is replacing this species in the forest composition.

In woodlands where competition for light is severe the tulip tree cannot compete with more shade tolerant species such as *Acer saccharum* and *Fagus grandifolia*. On the margins of forests, in open field sites, and in young stands its rapid growth and great size insure it a continuing place in the forest community. With selective management the tulip tree could be made to spread and develop in suitable areas in southwestern New York.

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The Limnology of Certain Prairie Lakes in Minnesota

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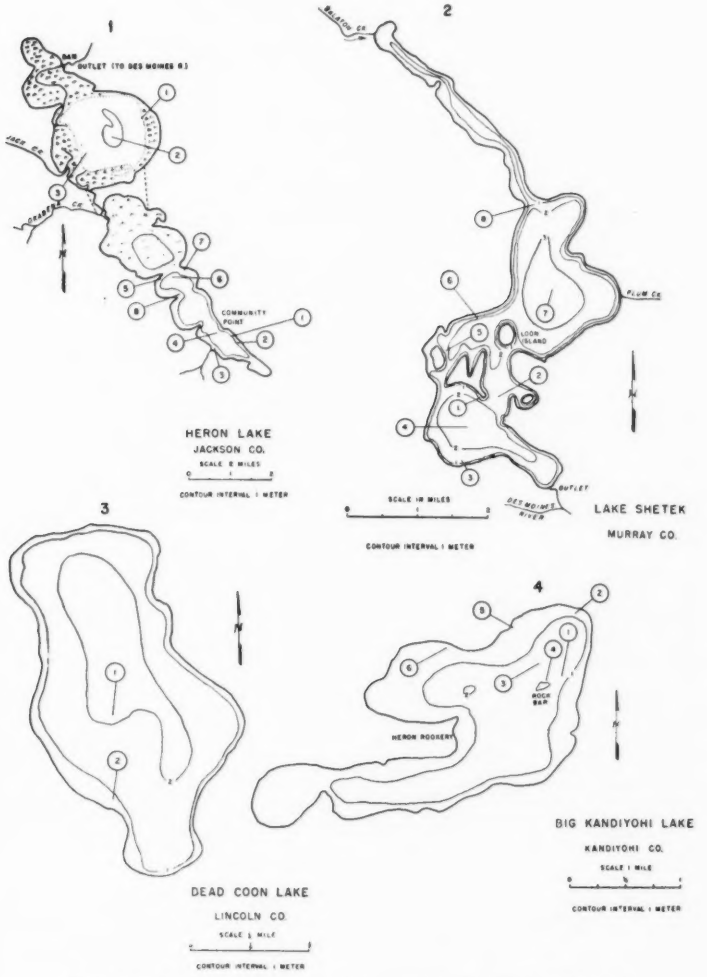
There have been few limnological investigations of shallow glacial lakes. Tressler and Domogalla (1931) made a comprehensive study of Lake Wingra, a small shallow lake near Madison, Wisconsin. Catlin and Hayden (1927) studied a small lake in Iowa. These investigators all emphasized the physiographic and botanical aspects of the lakes. Lindeman's outstanding work on Cedar Creek Bog Lake (1941) in Minnesota stressed the food-cycle relationships in this unusual eutrophic lake. He drew heavily for source material upon Naumann (1930-1931) and Thienemann (1925) who have contributed to our knowledge of lakes through their work in Europe. Their classification of lake types based on productivity still stands today, but Welch (1935) pointed out that it is entirely a European development based upon certain lake regions in Europe and that "no serious attempt has as yet been made to apply the classification to American lakes." Welch further indicated the need for more knowledge of conditions in American lakes before extensions of the classification could be attempted.

The greater part of the discussions which follow relates to the writer's investigations of four shallow prairie lakes in southwestern Minnesota during 1937-1938. The emphasis at that time was on physiographic features, physico-chemical factors and biological productivity as indicated by the "standing crop" of plankton and bottom fauna in these unique lakes. The more recent information was kindly provided by Dr. John B. Moyle and his associates of the Fisheries Research Unit, Minnesota Department of Conservation. Moyle stressed the physico-chemical factors and fisheries. The writer is also indebted to Dr. Moyle for his identifications of higher aquatic plants found in the lakes, to Dr. Samuel Eddy of the University of Minnesota, and to the late Dr. R. L. Lindeman for suggestions and helpful criticisms.

General Geology of the Region

A highland formation called the Coteau des Prairies lies in a diagonal position across southwestern Minnesota. When the last glaciation took place, the ice sheet was split by this highland formation. One lobe was deflected southeastward and advanced as far as Des Moines, Iowa. This lobe of the glacier has been named the Des Moines Lobe. The other glacial tongue was turned southwestward into South Dakota. In the path of the receding Des Moines Lobe of this Late Wisconsin Ice Sheet, there remains an undulating till plain which is interrupted by rather pronounced moraines. The lakes are situated in shallow depressions in the gray glacial drift. The topography is gently rolling and the soil is a rich black sandy loam of excellent quality for agriculture.



Figs. 1-4.—Lakes under study with contours based on 1937-38 levels.

METHODS

Beginning in the fall of 1937, collections were made from Heron Lake and from Lake Shetek. The surveys of Dead Coon Lake and of Big Kandiyohi were started in October and in February respectively. The field work was completed by May 1, 1938. Contour maps of the lakes, based on conditions of 1937-38, are presented in Figs. 1-4.

Water temperatures at top and bottom were determined by a maximum-minimum thermometer. Turbidity was read by a 30 centimeter Secchi disk. Chemical methods were those prescribed in *Standard Methods for the Examination of Water and Sewage,* 8th Ed. (1935). Except for total dissolved solids of the water and ash analyses of bottom muds, all physico-chemical analyses were performed in the field. Plankton samples of 100 liters or less were collected from the surface waters by means of a No. 20 silk bolting cloth net. Peterson and Ekman dredges were used with a No. 40-mesh screen used for sifting the material. Samples were preserved in 10 percent formalin.

GENERAL DESCRIPTION OF THE LAKES

HERON LAKE

Heron Lake is situated just north of the Minnesota-Iowa border in Jackson County (Fig. 1). Its area is 8,151 acres (1928). Three principal inlets enter the west side of the lake; a single outlet leaves the northeast side and joins the Des Moines River.

The history of Heron Lake is dramatic, as at one time waterfowl hunting here was famous throughout the Middle West. The shores of the northern part of the lake were bordered by extensive marshes suitable for breeding of many species of ducks and geese. As late as 1883, trumpeter swans were also observed to breed here.

About 1918, European carp were first noted in Heron Lake. In 1923 commercial fishing for this species was started and continued as a significant industry for many years. Concurrently, destruction of the choice aquatic plants was caused by the carp with resulting unfavorable conditions for sport fish and waterfowl.

The drought of the early 1930's caused the water level of this and other lakes in the area to drop to such an extent that depletion of dissolved oxygen in the winter under the ice became imminent. The winter of 1935-1936 was perhaps most serious in this regard, as the dissolved oxygen in Heron Lake water became depleted in February. This was at a time of extensive commercial fishing—seining under the ice—for carp. The carp were noted to be swimming feebly and apparently were near suffocation. Later when the ice melted, large numbers of dead fish were washed up on the beaches.

In the summer of 1936 a dam was constructed at the outlet of the lake and a four-foot head was maintained. The resulting inundation of large areas in the marshy north end of Heron Lake has restored much of the original feeding and nesting area for waterfowl.

At the time of these investigations, Heron Lake was divided into two parts by a broad strip of land. Formerly, this was undoubtedly a submerged sand bar. County maps drawn about 1918 show the lake basin in its entirety without this division. In 1937-1938, Division Creek, a narrow winding channel, connected the two parts of the lake on the west side. Heron Lake is the most shallow of the lakes under study. The deepest sounding obtained was 5 feet near Community Point, South Heron Lake. The bottom was of uniform contour.

LAKE SHETEK

Lake Shetek (Fig. 2) is located about 8 miles north of Slayton in Murray County. It is about 7 miles long and 2½ miles wide. Leverett and Sardeson (1919) reported a strong morainic system coming down from the northwest and sweeping around the south and east sides of the lake. The south and west sides of the lake constitute a broad till plain having a rich black clay-loam soil. A branch of the Des Moines River arises at the southeast side of the lake and flows southeastward to the main course of the Des Moines River. During high water, Balaton Creek flows into the northwest arm of Lake Shetek. When the lake was visited in August and September, 1937, this creek was dry.

The lake shores were lined with rocks and boulders of varying sizes. Willow trees grew among these rocks in a dense narrow row which surrounded most of the lake. The presence of the boulders along the shores was peculiar to Lake Shetek, unlike the other lakes herein described. Ice action probably has been responsible, but the presence of the rocks originally in the basin may be attributed to the kind of glacial till left in the moraine.

Lake Shetek was the deepest of the four lakes studied. A depth of 10 feet was recorded about one quarter of a mile southwest of Tipeota Beach on the north lake. In general, the bottom contour was found to be characteristically even. The shores were rocky and sandy and the bottom consistently muddy.

DEAD COON LAKE

Dead Coon (Fig. 3) Lake is situated near the center of Lincoln County about 8 miles north of Tyler. Like other lakes in this part of the state, Dead Coon lies in a narrow till plain between morainic ridges. Although no outlet stream was observed at low stage, at times of high water the lake drains to the Redwood and Minnesota Rivers. The occurrence of extensive growths of shrubs in one to two feet of water along the southwest shore in April, 1938, was evidence of still lower water level in the lake at an earlier date. Rough fish population was low at that time and local reports indicate Dead Coon Lake to be one of the most popular sport fishing lakes in the area. Maximum depth was about 8 feet with the bottom predominantly sand and gravel.

BIG KANDIYOHI LAKE

Big Kandiyohi (Fig. 4) Lake is situated about 9 miles southeast of Willmar in Kandiyohi County. The lake lies in a depression in the coarse, sandy till plain of the Keewatin glacier and was completely landlocked when first observed. During the drought the level of the lake dropped nearly 14 feet. The high banks lining the shore were indicative of the former high level of the lake. In July of 1938, Moyle reported that the maximum depth was 4 feet. The water was so saturated with hydrogen sulfide that it turned the zinc in galvanized pails black.

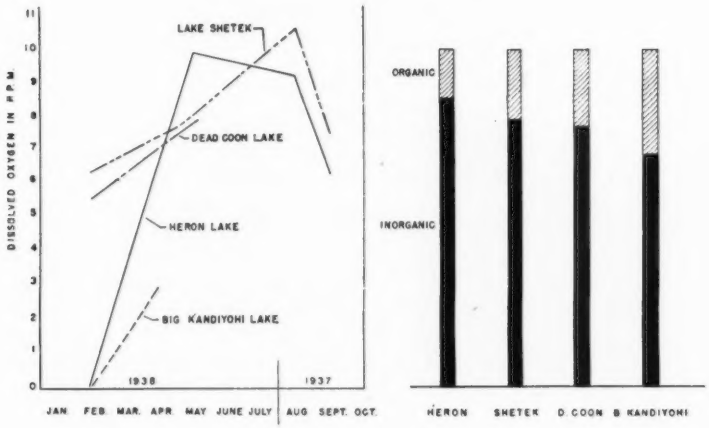
At one time, Big Kandiyohi was a popular resort lake with excellent sport fishing. However, since the drought and the ensuing winterkills of fish, it had not recovered sufficiently by 1937 to support a fish population.

PHYSICO-CHEMICAL FEATURES

DISSOLVED OXYGEN

Late summer and early fall records from Shetek and Heron lakes indicate high dissolved oxygen content of the waters: 6.0-10.8 ppm, but not so high as might be expected under the conditions of the algal production (see Fig. 5). Although the samples were collected during daylight hours, some diurnal fluctuations undoubtedly occurred.

Although marked and persistent physical or chemical stratification has rarely been reported in shallow lakes of this kind, a good example of short-term stratification was found in South Heron Lake. After a 12-hour period of calm, the dissolved oxygen content in surface waters was 12.89 ppm but only 5.4 ppm near the bottom at a total depth of less than 4 feet. After a short period of mixing by a sudden high wind, 8.84 ppm dissolved oxygen was found at the surface and 9.98 ppm at the bottom. Similar evidence of temporary stratification could not be found in Shetek or the other lakes under study.



Figs. 5, 6.—5. Seasonal fluctuations in dissolved oxygen. 6. Ratio of organic to inorganic matter in the ashed samples.

Heavy losses of water volume during the drought years just preceding these studies had overtaxed the dissolved oxygen resources beneath the ice of winter in Big Kandiyohi and Heron lakes. Larger areas of the former were found to be frozen to the bottom and, as indicated in Table I, the dissolved oxygen was depleted from South Heron and from Kandiyohi in February, and very nearly so from North Heron. Shetek and Dead Coon fared better as readings were 5 plus ppm at the time of the winter survey.

TABLE I.—Results of Chemical Analyses—February, 1938.

Lake	Dissolved Oxygen ppm	pH	Total Alkalinity ppm
Heron	0.0	6.6	338
Shetek	6.2	7.2	176
Kandiyohi	0.0	7.2	220
Dead Coon	5.3	6.9	275

TOTAL ALKALINITY

Total alkalinity was an extremely variable factor, but was highest in Heron and lowest in Shetek. In Heron, highest alkalinity occurred in winter with 338 ppm. The lowest reading was 120 ppm in Shetek for August (see Fig. 8 and Table II).

TABLE II.—Results of Chemical Analyses—August and September, 1937.

Lake	Temperature °C	Dissolved Oxygen ppm	pH	Total Alkalinity ppm
Heron	Aug. 27	9.2	8.4	150
	Sep. 25	6.0	8.4	160
Shetek	Aug. 24	10.8	8.8	120
	Sep. 22	7.4	8.8	125

The extreme variation of 150 ppm in August for Heron Lake in contrast with the 338 ppm for February is attributed to fluctuation in levels of photosynthetic activity, pulses of phytoplankton and presence or absence of ice cover. Generation of CO_2 in bottom muds and its retention under the ice is believed to be an important factor in the high total alkalinity in winter.

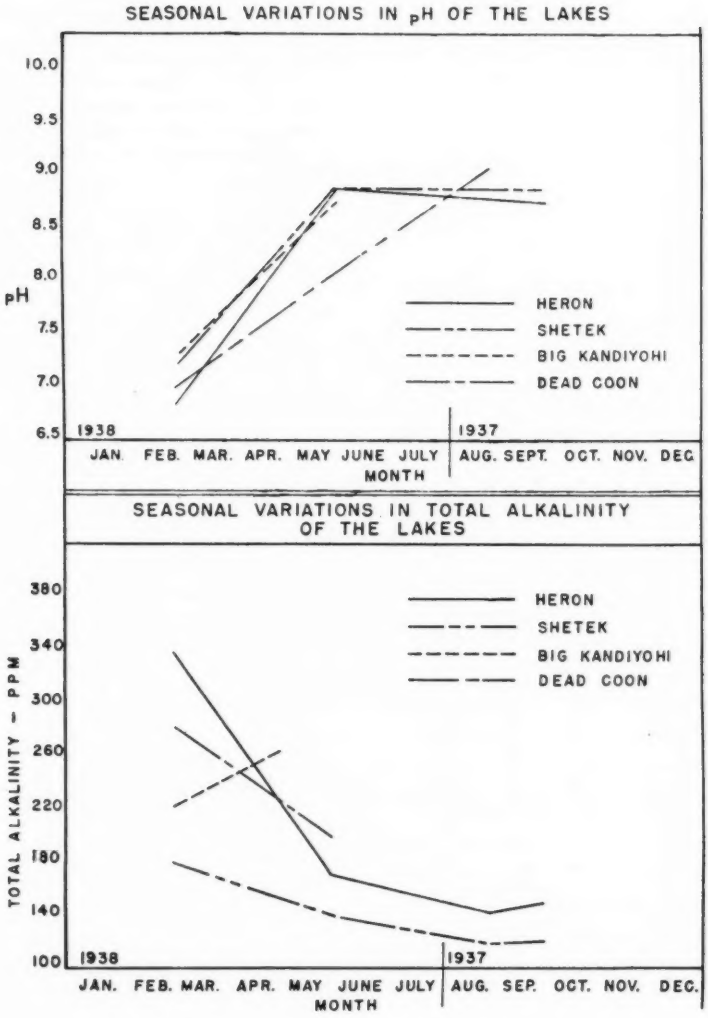
HYDROGEN ION CONCENTRATION

As indicated above, pH is closely correlated with the alkalinity regime of natural waters (Fig. 7). It is noteworthy that carbonic acid production under the ice in Heron was sufficient to lower the pH value to 6.6. Highest consistent values were found in Shetek with 8.8 at all times sampled when the lake was free from ice.

TOTAL DISSOLVED SOLIDS AND ASH ANALYSES

Reference is made to Table III which presents the complete data obtained from the spring survey. Table IV compares some of these results summarized along with data from Devil's Lake, North Dakota, an extreme prairie lake type (see Young, 1924).

In the matter of total dissolved solids, Kandiyohi's waters exceeded any other of the three lakes by more than four times with South Heron lowest at 335.8 and Kandiyohi 1991.6 ppm. However, Devil's Lake exceeded Kandiyohi six plus times with 13,462 ppm.



Figs. 7, 8.—Seasonal variations in the four lakes studied.

TABLE III.—Physico-chemical Data—Spring, 1938

Locality	Cm Secchi Disk	Temp. °C	Dissolved Oxygen ppm	pH
N. Heron	18.7	12.2	8.8	8.3
S. Heron	21.2	14.4	11.2	8.9
N. Shetek	70	10.8	7.2	8.8
S. Shetek	26	10.2	8.05	8.8
Big Kandiyohi	cloudy	8.0	3.0	8.7
Dead Coon	cloudy	14.4	7.9	8.1

TABLE III.—(*continued*)

Locality	$CaCO_3$ ppm	$Ca(H_2CO_3)_2$ ppm	Total Dissolved Solids ppm	Percent Ash Inorganic	Organic
N. Heron	17.5	177.5	429.0	89.95	10.05
S. Heron	22.5	137.5	335.8	81.81	18.19
N. Shetek	22.5	98.75	357.0	77.86	22.14
S. Shetek	22.5	100.0	453.4	79.89	20.11
Big Kandiyohi	18.75	252.5	1,991.6	67.05	32.95
Dead Coon	—	190.0	398.7	77.00	23.00

TABLE IV.—Comparison Between Devil's Lake and Minnesota Lakes in Chemical Analyses*

	Devil's	Shetek	Heron	Big Kandiyohi	Dead Coon
Normal carbonates, $CaCO_3$	305	22.5	22.5	18.75	—
Bicarbonates as $Ca(HCO_3)_2$	458	99.0	157	252.5	190
Total Solids	13,462	405	382	1,991	398
pH	10+	8.8	8.5	8.7	8.1

* Chemical Analysis for Minnesota Lakes is based on spring data.

Kandiyohi also exceeded all the other lakes in this study in regard to percent organic matter in its bottom deposits (Fig. 6). Almost one-third of the dry weight of bottom mud was organic in Kandiyohi with Dead Coon next with 23 percent and North Heron the least in organic content at 10 percent. The latter is attributed to the fact that North Heron was dry for a time earlier in the decade of the thirties and reflooded only after construction of the dam at the outlet. The persistent traces of oxygen under the ice in winter in North Heron despite extreme shallowness of the lake is attributed to the low organic content of the bottom deposits.

TABLE V.—Summarized results of plankton counts.

Group of Organisms	Predominant Species	Group Total Kofoid Units* In Thousands	Predominant Species	Group Total Kofoid Units In Thousands
		South Heron Lake		
	August 12, 1937		September 24-25, 1937	
Blue-Green Algae	*Microcystis flos-aquae*	240,000	*Microcystis flos-aquae*	295,000
Green Algae	*Pediastrum Boryanum*	18,000	*Pediastrum Boryanum*	28,000
Diatoms	*Melosira granulata*	18,000	*Melosira granulata*	29,000
Protozoa	*Ceratium hirundinella*	213	*Eudorina elegans*	2,000
Rotatoria	*Keratella cochearis*	3,700	*Keratella cochlearis*	1,600
Crustacea	*Cyclops leuckarti*	1,000	*Diaptomus siciloides*	3.8
	February 2, 1938		April 30, 1938	
Blue-Green Algae	*Lyngbya limnetica* *Oscillatoria* spp.	82	*Microcystis flos-aquae*	46,700
Green Algae	*Pediastrum Boryanum*	45	*Pediastrum Boryanum*	18,000
Diatoms	*Fragilaria capucina*	5.3	*Melosira granulata*	35,000
Protozoa	*Chlamydomonas sp.*	16.9	*Phacus* sp.	133
Rotatoria	*Polyarthra trigla*	18.9	*Polyarthra trigla*	284
Crustacea	.....	.....	*Cyclops leuckarti*	759
		North Heron Lake		
	February 2, 1938		April 30, 1938	
Blue-Green Algae	*Aphanizomenon flos-aquae*	8,800	*Oscillatoria* sp.	21,800
Green Algae	*Pediastrum Boryanum*	189	*Pediastrum Boryanum* *Scenedesmus dimorphus*	4,200
Diatoms	*Melosira granulata*	1,700	*Melosira granulata*	13,800
Protozoa	*Codonella cratera* *Difflugia urceolata* *Gonium pectorale*	142	*Chlamydomonas* sp.	1,400
Rotatoria	.....	.....	*Keratella cochlearis*	360
Crustacea	.....	.....	*Cyclops leuckarti*	125
		Lake Shetek		
	August 6 and 8, 1937		September 22 and 25, 1937	
Blue-Green Algae	*Oscillatoria* sp.	50,000	*Microcystis flos-aquae*	50,000
Green Algae	*Staurastrum* sp.	653	*Pediastrum duplex*	2,700
Diatoms	*Melosira granulata*	69,000	*Melosira granulata*	64,000
Protozoa	*Ceratium hirundinella*	828	*Glenodinium aciculiferum*	1,700
Rotatoria	*Keratella cochlearis*	945	*Keratella cochlearis*	914
Crustacea	*Cyclops leuckarti*	88	*Diaptomus siciloides*	29
	January 22 and February 4, 1938		April 24, 1938	
Blue-Green Algae	*Lyngbya limnetica*	4,500	*Lyngbya limnetica*	37,000
Green Algae	*Pediastrum Boryanum*	15	*Pediastrum Boryanum*	695
Diatoms	*Melosira granulata*	105	*Melosira granulata*	3,650
Protozoa	*Dinobryon sertularia*	85	*Synura uvella*	493
Rotatoria	*Keratella cochlearis*	349	*Polyarthra trigla*	1,050
Crustacea	*Diaptomus siciloides*	14	*Cyclops leuckarti*	23

* Owing to lack of space, complete tables of results of plankton and bottom fauna tests were not included. These data may be obtained on request from University of Minnesota Library.

BIOLOGICAL FEATURES

AQUATIC VEGETATION

Aquatic vegetation was extremely abundant at the north end of Heron Lake. The bulrush, *Scirpus acutus,* was most common in the open water. In the more protected places, the river rush, *Scirpus fluviatilis,* abounded. *Sparganium eurycarpum, Phragmites communis* and *Typha latifolia* were common in patches. Underneath these taller plants were found the following: *Utricularia vulgaris* var. *americana, Lemna minor, Spirodela polyrhiza, Potamogeton pectinatus* and *Polygonum coccineum.* In the open channels between heavy weed patches, the arrowhead, *Sagittaria cuneata,* might be found occasionally along with the narrow-leaved pond weed, *Potamogeton pectinatus,* and *Ceratophyllum demersum.*

Except for sparse patches of emergent aquatic plants along its shores, Lake Shetek was otherwise devoid of larger aquatic vegetation. These scattered groups of plants included *Scirpus acutus, S. fluviatilis, Phragmites communis, Polygonum natans* and *P. coccineum.* Among rocks lining the shores, the sedge, *Cyperus strigosus* was found in large numbers.

Higher aquatic plants were not found to be abundant at Dead Coon Lake. Of those found, the river rush, *Scirpus fluviatilis,* was most common. The bulrush, *S. acutus,* occurred in scattered patches. Among the submerged plants, *Potamogeton Richardsonii,* was found in large patches and *P. pectinatus,* although less abundant than the other pond weed, was present.

Heron Lake contained a heavy bloom of blue-green algae in the summer and autumn. Predominant organisms were *Microcystis flos-aquae* and *Oscillatoria* spp. Total numbers of blue-greens ranged as high as 460 million per cubic meter in South Heron which was approximately ten times the concentrations found in Shetek. Pelagic diatoms were represented in greatest numbers by *Melosira granulata.* Large numbers of the Volvocales organism *Eudorina elegans* (4.5 million) occurred in the September samples from South Heron. Although North Heron was not sampled until winter, the spring samples showed a strong beginning of the same kind of blue-green bloom that was getting underway in South Heron.

The winter plankton indicated the usual decrease in phytoplankton with consequent predominance of zooplankton. The abundance and diversity of the rotifers were noteworthy, with *Keratella cochlearis, Filinia longiseta* and *Brachionus angularis* most common. This is near the northernmost limit of the range for the genus *Brachionus.*

In Lake Shetek, the samples for August and September, as with Heron, indicated predominance of blue-green algae, but with different species present: *Oscillatoria* spp., *Anabaena circinalis* and *Lyngbya limnetica,* among several others. Although the blue-greens decreased in numbers during the winter, *Aphanizomenon flos-aquae* and *Lyngbya limnetica* maintained themselves successfully throughout the winter and were ready for resurgence in the spring. Among the zooplankton, the rotifers were again salient features with *Brachionus havanaensis* high in August and declining in September. *Brachionus angularis* appeared throughout the year in appreciable numbers.

Winter plankton in Kandiyohi was sparse, with a few *Chroococcus* sp. and *Oscillatoria* spp. representing the blue-greens and *Pediastrum boryanum*, the greens. The water under the ice had a brown, olive-green color which was attributed to the colloidal organic content of the water rather than to the chlorophyll or pigments of algae. There were but few zoöplanktonic organisms present under the ice. With the spring breakup and heightened water temperatures, there came a tremendous upsurge of algal activity in Big Kandiyohi with *Lyngbya limnetica* alone showing a concentration of 148 million filaments per cubic meter. *Lyngbya Birgei* and *Gomphosphaeria aponina* followed closely

TABLE VI.—Bottom fauna of South Heron Lake. Numbers per square meter.

	Station											
	1		2			3			4			
	Sept. 11, 1937	Apr. 30, 1938	Sept. 11, 1937	Oct. 25, 1937	Apr. 30, 1938	Sept. 12, 1937	Apr. 30, 1938	Sept. 12, 1937	Oct. 25, 1937	Apr. 30, 1938
Chironomids										
Chironomus digitatus	.....	31	31	43	.....	46	.....	109	.....	.....
C. tentans	899	.....	2,635	322	.....	.....	.....	10,416	7,600	280
C. lobiferus	1,798	.....	2,682	151	.....	5,332	47	.....	.....	22
C. flavus	868	.....	341	.....	124	93	140	.....	.....	.....
Chironomus sp.	.....	.....	.....	.....	47	.....	.....	.....	.....	.....
C. pupae	.....	.....	250	.....	.....	62	.....	.....	.....	.....
Tanytarsus sp.	.....	.....	2,635	.....	822	4,092	527	.....	.....	.....
Procladius adumbratus	248	202	.....	.....	62	.....	16	326	64	581
Other Diptera										
Chaoborus punctipennis	.....	.....	78	.....	.....	.....	.....	62	452	237
Palpomyia sp.	31	31	.....	.....	.....	31	.....	78	42	.....
Baetidae										
Caenis sp.	16	.....	.....	.....	16	31	16	.....	.....	.....
Hirudinea										
Glossiphonia nephheloidea	.....	.....	.....	.....	16	78	.....	.....	.....	.....
Phyllopoda										
Estheria mexicana	46	.....	.....	.....	.....	.....	.....	.....	.....	.....
Oligochaetes										
Limnodrilus sp.	.....	977	109	280	78	.....	1,395	.....	.....	22
Tubifex sp.	.....	233	.....	65	140	.....	682	.....	.....	22
TOTAL	3,906	1,474	8,761	861	1,305	9,765	2,823	10,991	8,158	1,164

behind with 31 million and 20 million respectively. The protozoan *Synura uvella*, which was unusual or at best not abundant in the other lakes, occurred in the spring with over 6 million colonies per 1000 liters. Diatoms also showed a spring pulse in this lake, but zooplankters were scarce at all times.

Dead Coon Lake, when first observed in October of 1937, had an extremely heavy bloom of *Aphanizomenon flos-aquae*. At that time of incipient ice formation many of the algal filaments were dying and disintegrating as evidenced by the light-green milky material washing up on the beaches. Unlike any other blue-green bloom in the other lakes under study, this was a case of absolute dominance by a phytoplankter. No other plankter was found at that time.

On May 1, 1938, the following spring, however, there was not a trace of *Aphanizomenon* to be found in Dead Coon; instead, a few greens, notably *Pediastrum Boryanum* (220,000), a fair pulse of diatoms, *Melosira* sp. (170,000) and some copepods and cladocerans were the sole representatives of the plankton. *Cyclops leuckarti* were checked at 45,000 and *Daphnia pulex* at 6,000 per cubic meter.

BOTTOM FAUNA

All four of the lakes under study, with the exception of Dead Coon, had productive sandy beaches and comparatively unproductive muck-ooze bottoms. Results of bottom sample analysis are presented in Tables VI-XI. The sampling locations may be found on the contour maps of the lakes. The habitat along the sandy beaches is subject to wave action in summer and ice thrust in winter. The fine soft muck bottoms of the lakes constitute a similarly rigorous environment wherein those animals which survive must either be adapted to life within the upper mud stratum with only part of their bodies protruding, such as with oligochaete worms; must be active enough to stay on or near the surface of the mud such as the midge larva, *Chironomus tentans;* or live largely independent of the bottom as does the phantom midge, *Chaoborus punctipennis*. In addition, where rough fish, such as carp, are present in numbers, their feeding habits of "mumbling" (Cahn, 1929) over the bottom constitute still another hazard to the bottom fauna. The organisms may be eaten by the carp or smothered by mud roiled up by the fish. This was particularly true of Shetek where chironomids and oligochaete worms were not found in any of the samples from the deeper sections of the lake. At Station 2, however, there was a large population of phantom midges—31,000 plus per square meter.

Many of the samples from the deeper waters of Shetek contained large numbers of fingernail clam shells (*Sphaerium* sp.) and small snail shells such as *Amnicola* spp. and *Valvata tricarinata*, but none was found living. A more varied fauna was found at such shallow beach Stations as 1, 3 and 6. Several species of midges were found along with some mayfly nymphs, *Caenis* sp.

Heron Lake had the largest population of bottom fauna of the four lakes. Strangely enough, North Heron had the only significant population of oligochaetes. South Heron had the largest population of midges of any of the lakes. Owing to the recent extensive fish kills, which have been devastating in Heron Lake, the reduction in rough fish has apparently allowed more free growth of bottom fauna than elsewhere.

TABLE VII.—Bottom fauna. Numbers per square meter.

	South Heron Lake								North Heron Lake				
	Station												
	5		6		7		8		1		2		3
	Aug. 13, 1937	Sept. 24, 1937	Aug. 13, 1937	Sept. 24, 1937	Aug. 13, 1937	Sept. 24, 1937	Aug. 13, 1937	Feb. 3, 1938	Feb. 2, 1938	Apr. 30, 1938	Feb. 2, 1938	Apr. 30, 1938	Apr. 30, 1938
Chironomids													
Chironomus digitatus	.....	.....	.....	.....	124	86	496	.....	108	.....	22	.....	.....
C. tentans	.....	43	915	280	.....	.....	1,318	86	323	44	581	194	.....
C. lobiferus	186	.....	.....	.....	.....	.....	155	.....	.....	.....	.....	.....	.....
C. flavus	124	31	.....	215	588	.....	.....	.....	.....	.....	.....	.....	.....
C. sp.	.....	.....	16	.....	.....	500	310	.....	.....	.....	.....	.....	.....
C. pupae	.....	.....	.....	.....	.....	.....	16	.....	.....	.....	.....	.....	.....
Procladius adumbratus	78	31	.....	.....	.....	.....	.....	43	43	.....	86	237	.....
Tanypus sp.	62	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Other Diptera													
Chaoborus punctipennis	31	.....	16	.....	16	.....	.....	86	.....	.....	.....	.....	.....
Palpomyia sp.	47	.....	109	.....	.....	.....	31	.....	22	22	43	44	.....
Baetidae													
Caenis sp.	.....	22	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Hirudinea													
Glossiphonia nepheloidea	16	.....	78	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Oligochaetes													
Limnodrilus sp.	93	43	16	.....	16	43	188	.....	452	129	258	3,078	258
Tubifex sp.	.....	.....	.....	.....	.....	.....	465	.....	2,799	44	2,067	3,875	.....
Amphipods													
Hyalella knickerbockeri	.....	.....	16	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
TOTAL	637	170	1,166	495	744	629	2,979	215	3,747	239	3,057	7,428	258

TABLE VIII.—Bottom fauna of Lake Shetek. Numbers per square meter.

	Station 1			2		3				4			
	Sept. 7, 1937	Oct. 22, 1937	Apr. 21, 1937	Sept. 6, 1937	Jan. 22, 1938	Sept. 6, 1937	Oct. 22, 1937	Jan. 22, 1938	Apr. 24, 1938	Oct. 22, 1937	Oct. 22, 1937	Jan. 22, 1938	Apr. 24, 1938
Chironomids													
Chironomus lobiferus	.....	.....	16	.....	.....	.....	.....	.....	47	.....	.....	.....	.....
C. digitatus	.....	.....	.....	.....	.....	.....	47	.....	.....	.....	.....	.....	.....
C. tentans	124	62	109	.....	65	31	62	194	.....	.....	.....	172	.....
C. flavus	419	16	279	.....	.....	78	.....	689	.....	.....	.....	.....	.....
Procladius adumbratus	.....	.....	16	.....	22	.....	.....	.....	.....	.....	.....	151	44
Tanytarsus sp. .	.....	.....	.....	.....	.....	.....	.....	.....	62	.....	.....	.....	.....
Other Diptera													
Chaoborus punctipennis	.....	16	47	31	474	16	62	.....	.....	323	538	495	344
Baetidae													
Caenis sp.	.....	.....	.....	.....	.....	.....	.....	.....	16	.....	.....	.....	.....
Oligochaetes													
Limnodrilus sp.	.....	.....	93	.....	.....	31	16	108	.....	.....	.....	.....	.....
Tubifex sp.	.....	.....	31	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
TOTAL	543	94	591	31	561	156	187	991	125	323	538	818	388

Numerous minute ostracods were found in the deeper bottom samples from Big Kandiyohi along with a few *Chironomus tentans, Procladius adumbratus* and oligochaete worms, *Limnodrilus* sp. By contrast, the sandy beach samples, Stations 2, 4, 5 and 6, were extremely rich in midges, predominantly *Tanytarsus* sp. Some scuds were also found along the sandy shores (*Hyalella knickerbockeri*).

Dead Coon Lake had a sandy bottom for the most part with midges and oligochaete worms predominating in deep as well as shallow samples. The

TABLE IX.—Bottom fauna of North Lake Shetek. Numbers per square meter.

	Station 5		Station 6				Station 7			Station 8		
	Sept. 8, 1937	Apr. 24, 1938	Sept. 8, 1937	Apr. 24, 1938	Sept. 8, 1937	Oct. 22, 1937	Feb. 4, 1938	Apr. 24, 1938	Oct. 25, 1937	Feb. 4, 1938
Chironomids										
Chironomus lobiferus	.....	.....	46	.....	.....	.....	.....	.....	.....	.....
C. digitatus	.....	.....	.....	.....	.....	.....	.....	.....	.....	16
C. tentans	171	.....	620	171	.....	.....	.....	.....	.....	140
C. flavus	1,891	.....	465	310	16	.....	.....	.....	.....	.....
Procladius adumbratus	.....	151	.....	124	.....	.....	.....	44	.....	78
Other Diptera										
Chaoborus punctipennis	.....	108	.....	62	.....	86	237	237	186	279
Oligochaetes										
Limnodrilus sp.	.....	22	.....	31	.....	.....	.....	.....	.....	.....
Tubifex sp.	.....	.....	.....	16	.....	.....	.....	.....	.....	.....
TOTAL	2,062	281	1,131	714	16	86	237	281	186	513

sand-bottom midge, *Chironomus lobiferus*, took the ascendancy over the mud midge, *Chironomus tentans*, so commonly found in the other lakes in the deeper areas.

MORE RECENT STATUS OF THE LAKES

Information as to the more recent status of the prairie lakes has been obtained from the Minnesota Department of Conservation, Fisheries Research Unit. During the interval between the author's studies and the more recent lake surveys of the Department of Conservation, there has been a series of years with ample rainfall. This is in contrast to the severe drought of the early and middle 1930's immediately preceding the author's investigations. As a result, all of the lakes contain more water than in 1937-1938.

South Heron is almost entirely open water and much of the middle and northern sections are open. There has always been considerable fluctuation in water levels but probably not much change in average levels since 1939. Removal of the dam at the outlet of Heron Lake around 1945 has caused the average level to drop 2 feet. Maximum depth in South Heron is 6 feet.

Although a winterkill of fish or near kill occurs almost every year in Heron, fertility is so high that fish populations quickly recover. Test netting by seine, gill net, and hoop net indicates that between 85 and 98 percent by weight of the fish are rough fish. Nevertheless a fair game fishery is provided by northern pike and bullheads. A total of over a million pounds of rough fish have been removed in 14 years of commercial operations.

TABLE X.—Bottom fauna of Big Kandiyohi Lake. Numbers per square meter.

	Station					
	1		2		3	4
	Feb. 1, 1938	Apr. 23, 1938	Feb. 1, 1938	Apr. 23, 1938	Apr. 23, 1938	Apr. 23, 1938
Chironomids						
Chironomus tentans	.....	86	.....	.....	64	.....
Procladius adumbratus	.....	387	.....	.....	150	16
Tanytarsus sp.	.....	.....	.....	13,368	.....	31
Tanypus sp.	.....	.....	.....	.....	86	16
Hirudinea						
Glossiphonia complanata	.....	.....	.....	.....	.....	16
Hemiptera						
Corixa sp.	43	.....	.....	.....	.....	.....
Ostracods	.....	.....	32,291	.....	51,600	.....
Oligochaetes						
Limnodrilus sp.	.....	.....	22	.....	.....	.....
Amphipods						
Hyalella knickerbockeri	.....	.....	.....	64	.....	171
TOTAL	43	473	32,313	13,432	51,900	250

TABLE XI.—Bottom fauna. Number per square meter.

	Big Kandiyohi Lake		Dead Coon Lake			
	Station					
	5	6	1		2	
	Apr. 23, 1938	Apr. 23, 1938	Feb. 4, 1938	May 1, 1938	Feb. 4, 1938	May 1, 1938
Chironomids						
Chironomus lobiferus	.....	.....	.....	108	3,681	10,075
C. digitatus	.....	.....	194	65	258	388
C. tentans	16	.....	108	.....	.....	.....
C. flavus	155	.....	.....	387	.....	.....
Procladius adumbratus	.....	.....	301	587	.....	.....
Tanytarsus sp.	25,079	.....	.....	.....	.....	.....
Tanypus sp.	.....	775	.....	.....	.....	.....
Other Diptera						
Chaoborus punctipennis	.....	.....	32	.....	.....	.....
Hemiptera						
Corixa sp.	.....	22	.....	.....	.....	.....
Gastropods						
Succinea sp.	.....	.....	22	.....	.....	.....
Oligochaetes						
Limnodrilus sp.	171	.....	1,787	969	1,055	3,193
Amphipods						
Hyalella knickerbockeri	109	44	.....	.....	.....	.....
TOTAL	25,530	841	2,444	2,116	4,994	13,656

These results indicate that Heron is predominantly a rough fish lake, despite all earlier attempts to plant game fish. The possibility of adopting a management policy for waterfowl has been suggested. Both portions of the lake should be considered in this policy. If waterfowl management is undertaken, carp removal would be desirable. In order to reduce the numbers of carp, it is estimated that more than 90 pounds per acre must be removed each year to keep up with the growth and reproduction of this species, unless severe winterkills reduce carp numbers.

Information on Big Kandiyohi Lake has been obtained from the results of a survey by the State Conservation Department in July, 1953. As already indicated, Big Kandiyohi was nearly dry in 1938, with a maximum depth recorded at 6 feet. At that time no inlet or outlet was found.

In 1953 the lake was found to be completely full and receiving water from several drainage ditches. The high water level has caused agitation for a lower level and drainage of adjacent lands. At levels above 1101.5, one of the ditches (located in Section 34), which normally drains into the lake, reverses direction and drains from Big Kandiyohi to Lake Lillian and thence to the South Fork of the Crow River. No outlet control structure has been

provided. The maximum depth of the lake is 18 feet, but 50 percent of the lake is less than 15 feet in depth.

The results of chemical analysis of water collected from the center of the lake on July 17, 1953, are as follows: Total alkalinity 192.5 ppm; sulphate ion 40.0 ppm; total phosphorus 0.032 ppm; total nitrogen 1.78 ppm. From this it is seen that Big Kandiyohi is a hard water lake of high fertility. Repeated occurrence of heavy blooms of algae further support this conclusion.

Fish population studies indicate good walleye and northern pike populations which have provided an active game fishery in recent years. An abundance of carp and other rough fish has instigated a removal program. In order to maintain a balanced fishery in this carp-game fish lake, plans call for planting walleye pike fry once every three years and each spring following a winterkill. The program of rough fish removal will be continued.

Although there have not been similar lake surveys made in recent years on lakes Shetek or Dead Coon, the following observations by the Minnesota Department of Conservation are included: Lake Shetek is full to overflowing and has been supplying good walleye, northern pike and crappie fishing. It has moderate to heavy algal blooms and a large bullhead population. Winter oxygen levels have usually been well above the critical range, except in 1951 when the dissolved oxygen fell in some parts of the lake to 0.2 ppm. There was, however, no serious fish kill. There has been little information on Dead Coon Lake except that it has not had a winterkill since 1949 and it is supplying considerable game fishing, mostly for bullheads. There are heavy algal blooms each year.

DISCUSSION

The lakes under study are similar to one another in many respects. All of them were situated in depressions in the gray drift of the Wisconsin glacier; all of them were less than ten feet in depth; all lacked chemical and thermal stratification; all produced heavy blooms of blue-green algae in summer; and all were threatened with depletion of dissolved oxygen in the winter.

An abundance of dissolved nutrients has fostered the production of heavy algal blooms. Thorough mixing and turbulence have created an environment for optimum development of these blooms. Ruttner (1953) states that the photosynthetic capacity of a lake is influenced by turbulent water movements, and that "in a mass of water thoroughly mixed by turbulence, all the phytoplankters enjoy the same average condition of light."

Although the interpretations of the 1937-38 results are based on the biomass present at the particular moments when samples were collected, that is, the standing crop, some pertinent conclusions may be drawn regarding lake classification. The "close superposition of the photosynthetic zone over the decomposition zone" (Welch, 1935), the abundance of dissolved nutrients including phosphorus and nitrogen, high organic content of bottom deposits, rapid decline in dissolved oxygen under the ice, heavy production of phytoplankton, all indicate the eutrophic type of lake, according to the classification of Naumann and Thienemann. The extreme shallowness of the lakes and encroachment of aquatic vegetation as in Heron Lake show an advanced stage of eutrophication.

According to Forel's classification, modified by Whipple (1927), these prairie lakes are temperate lakes of the third order. By this is meant their surface water temperatures vary above and below 4°C and the temperature of the bottom water is similar to that of the surface water as circulation is continuous except when frozen.

Although the observable trend of lake succession through the years usually proceeds in an orderly fashion from oligotrophy into eutrophy to advanced eutrophication culminating in dry land, climatic cycles appear to reverse the trend or at least to reduce sharply the rate of change from time to time. Such was the case with the prairie lakes in question. The earlier investigations marked a period of critically low water levels following the severe drought of the early and middle thirties. Prairie lakes throughout the Middle West suffered in varying degree. Many dried up, others were hastened along in their successional development toward marsh and dry land; still others, such as the ones in question, experienced winterkills of fish, concentration of dissolved salts and similar drastic environmental changes.

Advancement of the climatic cycle in the early and middle portions of the last decade (1940-1946) brought heavy increases in precipitation and raised water tables and lake levels over large areas of the country. The report of Moyle and his associates on Heron and Kandiyohi lakes in particular indicates high productivity of fish despite winterkills almost every year in Heron. Kandiyohi has freshened markedly as a result of dilution and has developed a sizeable game fish population.

According to Eddy (1938), Kandiyohi during the drought was classified, on the basis of fish propogation, as a "bullhead lake." Improvement in the lake as a habitat for fish has allowed it to be reclassified as a "bass-pan fish-walleye lake" with northern pike as a predator. The same is also true of Lake Shetek which has been supporting an appreciable game fishery. Heron and Dead Coon lakes, however, retain their standing as "bullhead lakes" owing to their propensity for "freezing out" in the winter.

SUMMARY

Four prairie lakes of southwestern Minnesota were studied in 1937-38 to determine some factors of fertility and biological productivity based on their standing crops of plankton and bottom fauna. Subsequent information has been provided on the more recent status of the lakes from the standpoint of physico-chemical factors of fertility and fish populations.

The lakes lie in till plain depressions between moraines of the late Wisconsin glacier. Lakes Shetek and Heron have both inlet and outlet, even during extreme drought, but Dead Coon and Kandiyohi are landlocked except at high water levels.

There is little tendency for chemical and thermal stratification except in winter under the ice.

The extreme shallowness of the lakes provides for "close superposition of the photosynthetic zone over the decomposition zone" throughout their entire basins as contrasted to the limitation of this condition to littoral areas as with deeper lakes. When this condition is combined with turbulence which

mixes the water mass thoroughly, allowing all phytoplankters the same average conditions of light, the stage is set for a high level of productivity.

The heavy algal blooms were composed predominantly of blue-greens: *Microcystis flos-aquae*, *Oscillatoria* sp., and *Lyngbya limnetica*.

"Freezing-out" or depletion of dissolved oxygen beneath the ice in winter was a common occurrence in all of the lakes except Shetek during the drought years. More recently, Heron is the only lake which "freezes-out" regularly each winter.

Bottom fauna was most abundant in Heron Lake and sparsest in Shetek. This is attributed to the small population of fish in Heron owing to drought winterkills in contrast to the large population of carp and other rough fish in Shetek which had been grazing on the bottom and consuming the fauna.

The lakes have been classified in three ways: (a) **advanced eutrophic** according to Naumann and Thienemann, (b) **temperate lakes of the third order** according to Forel and Whipple, and (c) Heron and Dead Coon as **"bullhead lakes"** and Shetek and Kandiyohi as **"bass-pan fish-walleye lakes"** according to Eddy.

Recent information from Moyle indicates some retardation of eutrophication as a result of a series of years with ample rainfall accompanied by heightened water levels.

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A Guide to the Flowering Plants and Ferns of the Western National Parks

Part 5. Angiosperms: Dicotyledons (Salicaceae)

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This is a continuation of *A Guide to the Flowering Plants and Ferns of the Western National Parks.*[1] In this part treatment of the dicotyledons is begun with the willow family, including poplars and willows. Completion of the study of this group was greatly facilitated by the aid of Dr. Carleton R. Ball, willow specialist of the U. S. Department of Agriculture, who gave freely of his time in the identification of more than two hundred specimens of willows collected in the western national parks. Dr. Ball also checked the manuscript and offered many helpful suggestions, for which grateful acknowledgment is made.

Salicaceae—Willow Family

The willow family, including the poplars and cottonwoods as well as the willows, consists entirely of woody plants, mostly erect shrubs and small to large trees. The leaves are alternate, usually with a pair of leaf-like or scale-like appendages (*stipules*) at the base of the petiole at its point of attachment to the stem. The flowers, reduced to the essential parts (a single pistil or [1—] 2 to several or many stamens), are borne in the axils of scale-like bracts (*scales*) which are more or less closely arranged on a slender axis to form a spike-like cluster (*ament*), the so-called "catkin" which is characteristic of this family of plants. Staminate and pistillate flowers are borne in separate aments on different plants (dioecious). The fruits, produced on the pistillate plants only, are small capsules which split along the sides to free numerous small seeds, each with a tuft of long silky hairs.

Key to the Genera

Leafblades usually ovate (or cordate) to broadly triangular (lanceolate in *P. angustifolia* and *P. trichocarpa*); winter buds covered by several scales; scales of aments with broad margins deeply lacerate into many slender teeth; stamens usually numerous, these (or the pistil in pistillate aments) borne on a cup-like disc; large or small trees .....(Poplar, Cottonwood) Populus

Leafblades linear or lanceolate to oblong or ovate; winter buds covered by a single scale; scales of aments with entire or slightly toothed margins; stamens mostly in groups of 2 (rarely 1, or in groups of 3 to 7), each group (or the pistil in pistillate aments) subtended by a gland at the base (not a cup-like disc); mostly erect or ascending shrubs or trees, or sometimes the stems prostrate and herb-like in arctic-alpine situations .....(Willow) Salix

[1] Part 1. Pteridophytes and Gymnosperms. Amer. Midl. Nat. 54:1-32. 1955. Part 2. Angiosperms: Monocotyledons (Alismaceae, Hydrocharitaceae, Sparganiaceae, Zosteraceae, Gramineae). *Ibid.*, 58:73-114. 1957. Parts 3 & 4. Monocotyledons to be completed in future numbers.

POPULUS (Cottonwood, Poplar)

KEY TO THE SPECIES[2]

Leafblades narrowly to broadly lanceolate or ovate, longer than wide, (3) 5 to 10 (15) cm long; petioles more or less rounded in cross section, seldom more than ½ as long as blade (becoming as long in *P. acuminata*); winter buds gummy, usually with a balsamic odor.

Leafblades distinctly tapering to both ends, green on both sides or slightly paler below; petioles very short or long.

Leafblades lanceolate, 5 to 15 cm long, 2 to 3.5 cm wide, gradually tapering to apex; petioles very short, usually less than 1/3 as long as the blades; Rocky Mountain parks and sparingly in the southwest at higher elevations .....(Narrowleaf cottonwood) *P. angustifolia*

Leafblades broadly lanceolate to ovate, 4 to 10 cm long, 2 to 5 cm wide, rather abruptly tapering to a long slender tip; petioles ½ to about as long as the blades; rare in the southwest. Probably a hybrid (*P. angustifolia* x *P. fremontii*, in our area) .....(Lanceleaf cottonwood) *P. acuminata*

Leafblades lanceolate to ovate, broad at base (not tapering to point at base), tapering to apex, green above, much paler below; petioles 1/3 to ½ as long as blades (or sometimes nearly as long).

Leaf petioles glabrous; capsules glabrous, borne on slender stalks to 3 mm long, splitting by 2 valves; Rocky Mountain parks .....(Balsam poplar) *P. balsamifera*

Leaf petioles more or less hairy; capsules finely softly hairy, nearly sessile; splitting by 3 valves; parks of the Pacific slope .....(Black cottonwood) *P. trichocarpa*

Leafblades broadly ovate (or roundish) to broadly triangular, as broad as or broader than long; petioles flattened near blade, as long as the blades or longer; winter buds slightly resinous, without balsamic odor.

Leafblades roundish to ovate, 2 to 6 cm long, rounded to somewhat pointed at base, abruptly short-pointed at tip, the margins finely toothed to nearly entire; petioles 3 to 7.5 cm long; the most widespread species in the western parks. (*P. tremuloides* var. *aurea*) .....(Quaking aspen) *P. tremuloides*

Leafblades broadly triangular, (3.5) 5 to 7 cm long, broadest near base, abruptly narrowed to long (or short) tip, the margins irregularly coarsely toothed; petioles 4 to 7.5 cm long; southwest parks. (*P. fremontii* var. *arizonica*, var. *pubescens*, var. *toumeyi*, and var. *wislizenii*) .....(Fremont cottonwood) *P. fremontii*

OCCURRENCE.—*Populus acuminata:* MV; *angustifolia:* Yl, GT, RM, MV, Z; *arizonica* (see *P. fremontii*); *balsamifera* (*P. tacamahaca*): G, Yl, RM; *fremontii* (*P. fremontii* var. *arizonica*, var. *pubescens*, var. *toumeyi*, var. *wislizenii*): S, MV, Z, GC; *hastata* (see *P. trichocarpa*); *tacamahaca* (see *P. balsamifera*); *tremuloides* (*P. tremuloides* var. *aurea*, var. *vancouveriana*): MK, O, MR, C, Yo, K, S, G, Yl, GT, RM, Z, GC; *trichocarpa* (*P. trichocarpa* var. *hastata*): MK, O, MR, C, Yo, K, S, G; *wislizenii* (see *P. fremontii* var.); *sargentii:* Yl.

SALIX (Willow)

KEY TO THE SPECIES

I. Leafblades linear to lanceolate or oblanceolate, mostly 4 to 10 (12) times as long as wide; aments borne on lateral leafy twigs; scales yellow, soon falling; filaments hairy, at least below; upright shrubs or trees.

Leafblades mostly 0.2 to 0.7 (1) cm wide, sessile or tapering to very short petioles; aments appearing after the leaves, sometimes in pairs or in 3's; stamens 2 to each scale; capsules hairy or glabrous; styles very short or none; along streams and in sandy alkali washes at lower elevations, commonly forming clumps. Section LONGIFOLIAE.

[2] Nomenclature here used is according to that recognized by E. L. Little, Check list of native and naturalized trees of the United States. Agriculture Handbook No. 41, U. S. Government Printing Office, 1953.

Shrubs 2 to 9 m high (or small trees up to 12 or 15 m high); leafblades mostly not toothed, somewhat silky-hairy, at least below; capsules hairy at maturity; stigmas about 1 mm long, divided to base.

Leafblades 4 to 8 cm long; twigs grayish; styles evident; Pacific slope parks ..... (C, Yo, S) *S. hindsiana*

Leafblades 1 to 3 cm long; twigs becoming reddish or purplish; styles practically none; southwest ..... (Z, GC) *S. taxifolia*

Shrubs 1 to 5 m high, often forming thickets; leafblades finely toothed or entire; capsules glabrous at maturity; stigmas short; style none.

Leafblades dark green above, whitish below, 4 to 7 (10) cm long, closely toothed or nearly entire; twigs brown to blackish; capsules 4 to 5 mm long.

Leafblades oblanceolate to narrowly elliptic, 6 to 15 mm wide; capsules nearly sessile.

Leafblades glabrous ..... (Yo, K, S, G, Yl) *S. melanopsis*

Leafblades hairy below ..... (Yo, G) var. *bolanderiana*

Leafblades linear, 2 to 4 (5) mm wide; capsules with stalks 0.5 to 1 mm long ..... (S, G) var. *tenerrima*

Leafblades green or gray-green on both sides, 5 to 12 cm long, 2 to 12 mm wide.

Leafblades entire or with few distant teeth, finely hairy or glabrous; capsules (4) 5 (6) mm long, sessile or the lower short-stalked; western species.

Leafblades finely fuzzy-hairy, at least below.

Leafblades 5 to 12 cm long, to 10 mm wide, at first silky-hairy, becoming finely appressed-hairy; capsules nearly sessile ..... (Yl, RM, MV, B, Z, GC) *S. exigua*

Leafblades very narrow, to 5 mm wide, permanently silky-hairy; capsules short-stalked ..... (RM, B) var. *stenophylla*

Leafblades glabrous.

Leafblades often yellowish-green, averaging shorter and narrower than in the species ..... (K) var. *nevadensis*

Leafblades darker green, larger than in the species ..... (Yo, S) var. *virens*

Leafblades finely toothed or entire, glabrous at maturity, often with a few long hairs when young; capsules 5 to 8 mm long, on short stalks 0.5 to 1.5 mm long when mature; east of Continental Divide ..... (G) *S. interior*

Leafblades (0.8) 1 to 3 cm wide, mostly distinctly petioled, the margins mostly finely gland-toothed and the petioles often glandular (in Sect. PENTANDRAE); aments appearing with the leaves; stamens (3) 5 to 7 to each scale; capsules glabrous (except when young in *S. gooddingii*), stalked; styles very short. PLEIANDRAE Sections.

Foliage appearing yellowish-green as a mass; twigs slender, yellowish, often somewhat drooping; leafblades finely gland-toothed, the petioles not glandular; stipules soon falling or none; aments (3) 4 to 6 (8) cm long; mostly trees to about 12 m high, or tall shrubs.

Twigs densely hairy when young; leafblades linear-lanceolate, 6 to 10 cm long, 0.8 to 1(1.5) cm wide, not or scarcely paler below, at first finely hairy, the petioles 0.5 to 1 cm long; capsules 5.5 to 7 mm long, on stalks 2 to 3 mm long, hairy when young; found at lower elevations in Sierra Nevada and southwest parks. Section NIGRAE. (*S. nigra* var. *vallicola.*) ..... (Yo, S, Z, GC) *S. gooddingii*

Twigs mostly glabrous; leafblades lanceolate to narrowly ovate, 5 to 12 cm long, 1.5 to 3 cm wide, green above, whitish below, smooth, on petioles (0.5) 1 to 2 cm long; capsules 4 to 5 mm long, on stalks 1 to 2 mm long; Rocky Mountains, at lower elevations than most of the park areas. Section TRIANDRAE ..... (G) *S. amygdaloides*

Foliage appearing dark green as a mass, the leafblades smooth and shining above; twigs and buds mostly stout; branchlets lustrous, reddish-brown (or yellowish); stipules present or soon falling; aments 2 to 5 cm long; trees or shrubs.

Petioles without wart-like glands; leafblades shallowly toothed or nearly untoothed, pale or whitish below and often yellowish-hairy when young; scales woolly at base; capsules 3.5 to 5 mm long, on stalks 1.5 to 3 mm long; mostly trees or tall shrubs; Sierra Nevada and southwest parks. Section BONPLANDIANAE.

Twigs and petioles glabrous .....(Yo, Z) *S. laevigata*

Twigs, petioles, and lower midrib densely hairy .....(Yo, GC) var. *araquipa*

Petioles with wart-like glands at upper end below blade; leafblades mostly finely gland-toothed, mostly glabrous; scales thinly hairy at base; capsules 4.5 to 10 (12) mm long, on stalks 1 to 2 mm long. Section PENTANDRAE.

Clustered shrubs to 4 m high, commonly found in bogs or swampy places; leafblades elliptic-lanceolate, 4 to 8 cm long, 1 to 2.5 cm wide, short-pointed at tip, paler or somewhat whitish below; petioles slender; aments short, stout, fruiting in late summer; capsules 7 to 9 (12) mm long, thick-walled, shiny olive-brown or darker; found east of Continental Divide .....(G, RM) *S. serissima*

Small trees to 15 m high, or sparingly clustered shrubs to 5 or 8 m high, commonly found along streams; leafblades broadly to narrowly lanceolate, 5 to 13 cm long, (0.7) 1 to 3.5 cm wide, with long tapering points; petioles stoutish; aments 2 to 5 cm long, fruiting in early summer; capsules 4.5 to 7 mm long, thin-walled, light brownish to pale straw-color; found west of Continental Divide.

Leafblades slightly paler but not whitish below; stipules small or none; capsules on stalks 1 to 1.5 mm long; more or less clumped shrubs found in Rocky Mountains (and southwest parks).

Leafblades to 13 cm long, 1.2 to 3 cm wide; aments stout, 2 to 5 cm long.

Young branchlets, bud scales, and petioles soft-hairy .....(G, Z) *S. caudata*

Young branchlets, bud scales, and petioles soon becoming glabrous .....(G, Yl, GT, RM) var. *bryantiana*

Leafblades to 8 cm long, 0.7 to 1 (1.2) cm wide; aments rather lax, 2 to 3 (3.5) cm long .....(G, Yl, GT) var. *parvifolia*

Leafblades green above, whitish below; stipules often conspicuous, roundish, about 1 to 2 cm broad; capsules on stalks 1.5 to 2 mm long; commonly trees 5 to 15 m high, found mostly in Pacific slope (and southwest) parks.

Leafblades lanceolate to broadly lanceolate, 1.5 to 3.5 cm wide, with closely gland-toothed margins; petioles glandular; aments about 4 cm long.

Branchlets glabrous or nearly so .....(O, MR, K, S, Yl, B) *S. lasiandra*

Young branchlets densely soft-hairy .....(O, MR, K, S) var. *lancifolia*

Leafblades narrowly lanceolate, 1 to 1.7 cm wide, with shallowly toothed to nearly entire margins; petioles scarcely glandular; aments 2 to 3 (4) cm long .....(C, Yo) var. *abramsii*

II. Leafblades broader in proportion to length (or if longer, the margins usually not gland-toothed or the capsules are hairy or woolly); petioles not glandular; aments appearing before or with the leaves, stalked or sessile; scales yellowish to dark brown or black, persistent; stamens 2 (or 1 in Section SITCHENSES), the filaments glabrous or hairy.

a. *Upright shrubs or trees, or if low, the main stems not prostrate or rooting; scales of catkins long-hairy (except in Section* CORDATAE).

Twigs densely hairy with long straight or wavy white hairs (except var. of *S. alaxensis*); stipules evident, often conspicuous; aments appearing before the leaves, not stalked or scarcely so; scales brown; capsules glabrous or hairy, not stalked; styles 1 to 2.5 mm long; low or tall shrubs (or sometimes tree-like). Section LANATAE.

Leafblades densely white-felty hairy or silky-woolly (at least below) at maturity, linear-lanceolate to elliptic-oblong or oblanceolate, narrowed towards base; capsules hairy; far north (MK).

Shrubs or tree-like, to 9 m high; stipules long, narrow, long-hairy; leafblades 2 to 10 cm long, dark green above, conspicuously white-felty below.

Twigs and bud scales densely hairy ..... *S. alaxensis*

Twigs glabrous, covered with a bluish bloom ..... var. *longistylis*

Low shrubs 0.3 to 1.5 m high; stipules short, broad, with gland-toothed margins; leafblades 4 to 7 cm long, light green and silky-hairy on both sides.

Leafblades 1 to 2 cm wide ..... *S. barrattiana*

Leafblades characteristically narrower ..... var. *angustifolia*

Leafblades becoming smooth on both sides at maturity, broadly oval or ovate to obovate, rounded to somewhat narrowed at base, with finely gland-toothed margins; petioles 0.8 to 1.5 cm long; capsules glabrous or at least becoming so in age; low shrubs; Rocky Mountains and north.

Leafblades green on both sides, to about 7.5 cm long, to about 3.8 cm wide; petioles and midribs finely hairy; stipules conspicuous, ovate, clasping; northern Rocky Mountains (*S. barrattiana* var. *tweedyi*) ..... (G, Yl, GT) *S. tweedyi*

Leafblades yellowish below, to about 5.5 cm long, to 3 cm wide; petioles and midribs yellowish; stipules long, narrow; far north ..... (MK) *S. richardsonii*

Twigs glabrous or finely hairy or woolly, not densely long white-hairy; stipules present or none; scales of catkins brown to nearly black, (or tawny or yellowish); capsules stalked or sessile; styles present or none; shrubs or trees.

Capsules glabrous (sometimes finely or thinly hairy in *S. lasiolepis* and in var. of *S. wolfii*); scales brown to black.

Styles 1 to 1.5 mm long; leafblades oval or elliptic to ovate or narrowly obovate, (3) 5 to 8 (12) cm long, (1.5) 2 to 4 (5) cm wide, more or less hairy at first, at least above; stipules large (or none); northwest and Rocky Mountain parks. Section COMMUTATAE (Adenophyllae).

Young twigs finely hairy or becoming glabrous, brown to blackish; leafblades to 8 cm long, to 3 cm wide; the margins finely gland-toothed to entire; stipules large, gland-toothed; aments borne on leafy stalks 1 to 4 cm long, appearing with the leaves; capsules on stalks about 1 mm long (or slightly less); styles 1 to 1.5 mm long; rounded shrubs (0.5) 1 to 4 m high; mostly northwest (and Rocky Mountains).

Leafblades dark green above, whitish below, thinly hairy above, becoming smooth; scales blackish, long-hairy .... (MK, O, MR, G, Yl, RM) *S. barclayi*

Leafblades grayish-green and hairy on both sides, or becoming nearly glabrous; scales brownish, woolly.

Shrubs 1 to 3 m high in northwest and northern Rocky Mountains; leafblades 6 to 8 cm long, not toothed or scarcely so; stamens with filaments glabrous ..... (O, MR, G) *S. commutata*

Shrubs 1.5 to 2 m high in Sierra Nevada and Cascade Mountains; leafblades 4 to 6 cm long, more or less gland-toothed; stamens with filaments hairy below ..... (C, Yo, K, S) *S. eastwoodiae*

Twigs glabrous and shining, yellowish to reddish-brown; leafblades to 7 (or 12) cm long, 2 to 4 (5) cm wide, mostly glabrous at maturity; stipules present or none; aments not stalked or rarely very short-stalked with few leafy bracts, appearing before or with the leaves; capsules stalked or not stalked; styles 0.6 to 1. 5 mm long; low or tall shrubs in Rocky Mountains (and northwest).

Leafblades (4) 6 to 12 cm long, 2 to 5 cm wide, the margins finely gland-toothed or entire; stipules usually none, at least not persistent; capsules on stalks 1 mm long, styles 1 mm long; shrubs 5 to 6 m high; humid Transition Zone along Pacific coast ..... (O, MR) *S. piperi*

Leafblades generally smaller, 5 to 7 cm long, 2 to 4 cm wide, usually finely toothed; stipules large, usually persistent; Rocky Mountains at relatively high elevations.

Shrubs 3 to 6 m high; leafblades on flowering branches prevailingly narrowly obovate to oblanceolate; buds large, 1 cm long, beaked; capsules not stalked or scarcely so; styles 1 to 1.5 mm long .....(RM) *S. monticola*

Shrubs 1 to 3 m high; leafblades prevailingly broader on flowering branches; capsules on stalks 1 to 1.5 mm long; styles 0.6 to 1 mm long.

Leafblades mostly ovate on flowering branches; aments not stalked .....(G, Yl, RM) *S. pseudomonticola*

Leafblades mostly oval on flowering branches; aments on short leafy stalks .....(RM) var. *padophylla*

Styles less than 1 mm long; leafblades less than 2 cm wide or if broader, then glabrous or nearly so on both sides.

Leafblades mostly less than 2 cm wide, finely hairy or silky-hairy at least below, or becoming glabrous; stipules small or none; aments appearing before or with the leaves; scales long-hairy outside; capsules stalked or not stalked.

Leafblades oblanceolate or elliptic, pointed at tips, rounded at base, 2 to 6 cm long, 0.8 to 1.8 cm wide, not toothed, dull green on both sides; aments appearing before or with the leaves; low shrubs to about 1.5 m high; Rocky Mountains. Section WOLFIANAE.

Leafblades 2 to 4.5 cm long, 0.8 to 1.2 cm wide; fruiting aments 1 to 2.5 cm long, nearly globose to oblong; capsules glabrous; stems erect with widely spreading branches .....(RM) *S. wolfii*

Leafblades 3 to 6 cm long, 1 to 1.8 cm wide; fruiting aments to 3.5 cm long; capsules thinly hairy .....(Yl, GT) var. *idahoensis*

Leafblades narrowly lanceolate to narrowly or broadly oblanceolate, 6 to 10 cm long, 0.7 to 1.7 (2) cm wide, entire or somewhat wavy-toothed, dark green above, whitish below; aments appearing before the leaves; shrubs or trees. Section LASIOLEPES.

Shrubs 2 to 3 m high; twigs usually with a bluish bloom, glabrous or finely hairy when young; leafblades linear-lanceolate to linear-oblanceolate, 0.7 to 1.7 cm wide, glabrous on both sides; capsules glabrous, 3 to 4 mm long; Rocky Mountains, not common in the parks .....(RM) *S. irrorata*

Shrubs or small trees to 6 (10) m high; twigs usually finely hairy; leafblades narrowly to broadly oblanceolate, 1 to 2 cm wide, silky-hairy below or becoming glabrous: capsules glabrous or finely hairy, 4 to 4.5 mm long; Pacific slope parks (and southwest) ....(MR, Yo, S, Z) *S. lasiolepis*

Leafblades 1 to 3.5 cm wide, broadly lanceolate, ovate, or elliptic to narrowly obovate or oblanceolate (or linear to lanceolate), mostly glabrous on both sides (or somewhat hairy when young); stipules usually present (or none in *S. farrae*); aments appearing with the leaves, on more or less leafy stalks; scales thinly hairy outside to nearly glabrous; densely hairy inside in *S. mackenziana*); capsules distinctly stalked; low to tall shrubs or small trees. Section CORDATAE.

Leafblades green on both sides, sometimes slightly paler, but not whitish below, usually finely gland-toothed (or scarcely toothed), broadly lanceolate or ovate to broadly oblanceolate or obovate, 3 to 7 cm long, 1 to 3.5 cm wide; stipules usually present; scales thinly long white-hairy.

Leafblades thickish or at least firm, 1 to 2 cm wide, pointed or blunt at the tips, on petioles 2 to 8 mm long; stipules lanceolate to ovate or none; aments 2 to 3 cm long; capsules on usually finely hairy stalks 1 to 1.5 mm long; stigmas thick, not divided; filaments of stamens free.

Shrubs 1 to 3 m high; leafblades pointed at tips, on petioles 3 to 8 mm long; stipules present; styles 1 or more mm long; widespread in parks of middle latitudes. (*S. pseudomyrsinites*, in part) .....(MK, C, L, Yo, K, S, G, RM) *S. pseudocordata*

Shrubs mostly less than 1 m high; leafblades blunt at tips, the petioles 2 to 4 mm long; stipules soon falling or lacking; styles 0.3 to 0.5 mm long; far north and southward on east side of Rocky Mountains. (*S. pseudomyrsinites*, in part) .....(MK, G, Yl, RM) *S. myrtillifolia*

Leafblades thinnish, 1.5 to 3.5 cm wide, pointed at tips, on petioles (4) 6 to 14 mm long; stipules broadly ovate or crescent-shaped; aments to 6 cm long; capsules on glabrous stalks 2 to 4 mm long; styles 0.3 to 0.7 mm long; stigmas usually divided; filaments of stamens united for 1/3 to 3/4 their length; shrubs 1 to 3 m high. (*S. pyrifolia* of w. floras) .....(G, Yl) *S. monochroma*

Leafblades distinctly paler or whitish below, entire or finely gland-toothed, broadly or narrowly lanceolate to obovate or oblanceolate (or linear in var. of *S. lutea*), 3.5 to 10 cm long, 1 to 4 cm wide; stipules ovate to crescent-shaped (or none); scales thinly hairy to glabrous (densely hairy inside in *S. mackenziana*).

Shrubs (or small trees) 2 to 6 m high; leafblades lanceolate (or linear) to narrowly ovate or oblanceolate, to 8 (10) cm long; widespread in parks of middle latitudes.

Twigs mostly yellowish; leafblades generally yellowish-green, 1.5 to 4 cm wide; capsules on stalks 0.5 to 2 mm long. (*S. watsonii* of park lists) .....(MR, GT, RM, B, Z) *S. lutea*

Twigs dark; leafblades dark green.

Leafblades 1 to 2 cm wide, to 10 cm long; scales thinly hairy; capsules on stalks 0.7 to 2 mm long .....(Yo, S. GC) var. *ligulifolia*

Leafblades 2 to 3.5 cm wide, to 7 cm long, usually gland-toothed; scales of catkins densely white-hairy on the inside; capsules on stalks 3 to 4 mm long. (*S. cordata* var.) .....(MR, Yo, S, G, Yl) *S. mackenziana*

Low clustered shrubs usually less than 2 m high (0.3 to 1.5 m high); leafblades elliptic-lanceolate to obovate, to 8 cm long, 2 to 3.5 cm wide; capsules on stalks to about 1.5 mm long; northern Rocky Mountains and far north.

Young twigs yellowish, glabrous (or at first very finely hairy); stipules very small or none; leafblades to 6 cm long, 1 to 2 cm wide; fruiting aments 2 to 3.5 cm long; scales thinly hairy to glabrous; styles 0.4 to 0.8 mm long; northern Rocky Mountains .....(G, Yl) *S. farrae*

Young twigs usually brown, more hairy (or becoming glabrous); stipules 2 to 6 (8) mm long; leafblades to 8 cm long, 2 to 3.3 cm wide; fruiting aments 4 to 5 cm long; scales nearly glabrous outside; styles almost none; far north. Section BALSAMIFERAE .....(MK) *S. walpolei*

Capsules hairy, silky, or woolly; scales dark brown to tawny or yellowish.

Leafblades lanceolate to elliptic or narrowly obovate; usually gray-hairy or fuzzy on both sides, or sometimes on upper surface only (or becoming glabrous), the margins entire; twigs rather stout, thinly to densely hairy or fuzzy-woolly, at least when young; aments appearing with the leaves, on short leafy stalks; scales long-hairy; styles evident, 0.5 to 1.5 mm long. Section GLAUCAE (Arcticae).

Leaves distinctly petioled, rather lax or spreading, leafblades 4 to 6 (8) cm long, 1.5 to 2.5 cm wide, more or less pointed at both ends or somewhat rounded at base, mostly more or less grayish-hairy or -woolly, especially below; stipules lanceolate or ovate, 0.5 to 1 cm long, on shoots of the season; scales oblong to narrowly oblong, pale to dark brown; capsules densely gray-woolly.

Shrubs commonly forming loose clumps 1 to 3 m high or sometimes tree-like and reaching 5 m; leafblades dark green above, whitish below, the twigs and young leaves usually densely hoary or woolly; stipules lanceolate; staminate aments 2 to 3 cm long; fruiting aments to 7 cm long; capsules 5 to 8 (10) mm long; far north .....(MK) *S. glauca* and vars

Young twigs densely white-hoary; leafblades densely whitish- or gray-woolly on both sides, or becoming nearly glabrous above.

Leafblades rather gradually narrowed to points at both ends; capsules to 8 mm long .....var. *acutifolia*

Leafblades broader towards base; capsules to 10 mm long .....var. *aliceae*

Young twigs very finely hairy to nearly glabrous; leafblades glabrous or nearly so, broader towards tips .....var. *glabrescens*

Low shrubs 1 to 1.5 m high; leafblades light green on both sides, generally paler below but not whitish, densely finely hairy or becoming glabrous above; twigs finely hairy, becoming glabrous; stipules narrowly to broadly ovate; aments generally smaller, the fruiting to about 4 (5) cm long; capsules to about 6 (7) mm long; Rocky Mountains. (*S. glaucops* and var. *glabrescens* of western floras.) .....(G, Yl, GT, RM) *S. pseudolapponum*

Leaves mostly very short-petioled, more or less erect and overlapping, forming "tufts" at the ends of branches, the blades 2 to 5 (6.5) cm long, 0.6 to 1.5 (2) cm wide, more or less pointed at both ends or somewhat blunt at tips, finely silky or woolly or becoming glabrous, light green on both sides or sometimes paler below; stipules small, more or less oval to ovate, or none; scales of catkins oval or oblong to narrowly obovate. The following 4 species are not clearly distinguished from *S. pseudolapponum*.

Bushy shrubs 0.5 to 2 (3) m high; young twigs finely silky-hairy; leafblades 3 to 5 (6.5) cm long, 0.8 to 1.5 cm wide, more or less densely silky-hairy or becoming nearly glabrous; stipules small but evident; fruiting aments 2 to 5 cm long; scales dark brown; capsules finely hairy, more or less stalked; styles to about 1 mm long.

Pacific slope species; fruiting aments to about 5 cm long; stalks of capsules to 1 or 1.5 mm long .....(C, Yo, K, S) *S. orestera*

Rocky Mountains; fruiting aments to about 3.5 cm long; stalks of capsules short, less than 1 mm long. (*S. stricta* of auth.) .....(Yl, GT, RM) *S. desertorum*

Low shrubs usually less than 1 m high; twigs finely fuzzy or woolly; leafblades 2 to 4 (4.5) cm long, 0.6 to 1.2 cm wide, somewhat whitish- or bluish-waxy below, finely woolly below or becoming glabrous; stipules none or soon falling; aments mostly shorter, (0.5) 1 to 2 cm long; scales yellowish to pale brown; capsules finely gray- or whitish-woolly, sessile or very short-stalked.

Leafblades to 1.2 cm wide, finely yellowish-woolly, mostly blunt at tips.

Aments mostly short, to about 1 cm long, on short stalks; capsules finely gray- or whitish-woolly; styles to 1.5 mm long; Rocky Mountains. (*S. stricta* of auth.) .....(G, Yl, GT, RM) *S. brachycarpa*

Aments longer, on longer stalks; hairs of leaves longer and less dense; leafblades more whitish-waxy below; styles less than 1 mm long .....(MK) var. *mexiae*

Leafblades narrower, pointed, softly whitish- or gray-hairy; styles 0.5 mm long, (resembling *S. brachycarpa* var. *mexiae*) .....(MK) *S. niphoclada*

Leafblades lanceolate or oblanceolate to ovate or obovate, more or less glabrous or thinly hairy on both sides or densely silky or woolly on lower surface only, toothed or sessile; twigs glabrous or hairy; aments appearing before or with the leaves, stalked or not stalked; scales more or less hairy.

Leafblades hairy or becoming glabrous at maturity, shiny or dull green above, mostly paler or whitish below, never densely white-woolly or silky; shrubs or small trees.

Leafblades narrowly elliptic to broadly oblanceolate, 2 to 4 (5) cm long; dull green; stipules none; aments appearing with the leaves; scales linear-oblong to narrowly lanceolate, yellowish to tawny, or sometimes reddish at tips, more or less hairy; capsules tapering into slender beaks, on stalks 2 to

5 mm long; styles very short or none; shrubs or small trees to 5 m high. Section ROSTRATAE (Fulvae).

Erect shrubs (or small trees) 2 to 5 m high; twigs brown to blackish, smooth or finely hairy; leafblades elliptic-oval to obovate, pointed at both ends, 1 to 2.5 cm wide, dull green above, paler below, strongly net-veined below; fruiting catkins 2 to 5 cm long, lax; scales yellow; capsules on slender stalks 2 to 5 mm long.

Leafblades 2 to 5 cm long, more or less finely hairy .....(MK, G, Yl, RM, Z, GC) *S. bebbiana*

Leafblades smaller, 2 to 3.5 cm long, nearly glabrous .....(MK, G, Yl, RM) var. *perrostrata*

Low shrubs 1 to 2 (3) m high; twigs blackish, mostly covered with a powdery bloom; leafblades narrowly oblanceolate, 0.5 to 1 cm wide, dark green above, whitish below, not strongly net-veined below; fruiting aments roundish, 1 to 2 cm long; scales tawny, with reddish tips; capsules on stalks 2 to 2.5 mm long.

Twigs glabrous; leafblades thinly silky-hairy or becoming glabrous above.

Twigs covered with whitish bloom; leafblades thinly hairy on both sides; Rocky Mountains and southwest .....(G, Yl, GT, RM, Z) *S. geyeriana*

Twigs without a bloom; shrubs becoming taller than species; leafblades becoming glabrous above, somewhat brownish-hairy below; northwest .....(MR) var. *meleina*

Twigs finely hairy; leafblades more densely and permanently silvery-hairy on both sides; Sierra Nevada and Rocky Mountains .....(Yo, K, S, Yl, RM) var. *argentea*

Leafblades ovate or obovate to lanceolate or narrowly oblanceolate, 2 to 10 (12) cm long, rather thickish or firm; aments appearing before or with the leaves; scales ovate to narrowly obovate, brown to black, long-hairy; capsules sessile or on short stalks not exceeding 2 mm (except *S. petiolaris* in Section PHYLICIFOLIAE); widespread in the parks.

Shrubs or small trees 4 to 10 m high; leafblades 3 to 10 (12) cm long, 1.5 to 3.5 cm wide, dark green and nearly glabrous above, whitish and silvery-hairy below or becoming rusty-hairy to glabrous; stipules small, or large with broad ear-like base; capsules tapering to slender beaks, on stalks 1 to 2 mm long; styles none. Section CAPREAE.

Aments appearing before the leaves; the most widespread species in the western parks .....(O, MR, C, Yo, K, S, G, Yl, GT, RM, Z, GC) *S. scouleriana*

Aments appearing with the leaves .....(L) var. *coetanea*

Low or tall shrubs 0.5 to 5 m high (some becoming tree-like); leafblades mostly 2 to 6 (9) cm long, (0.5) 1 to 2 (3.5) cm wide, shiny bright green above, paler or whitish below, nearly glabrous at maturity, the margins finely toothed to nearly entire; stipules mostly none or soon falling, or if persistent, then long and narrow; capsules not decidedly long-beaked, stalked or not stalked; styles evident. Section PHYLICIFOLIAE.

Low shrubs (sometimes somewhat prostrate) 0.5 to 1 (or 2) m high; buds conspicuous, ovate, chestnut brown, glabrous; leafblades broadly elliptic or ovate to obovate or broadly oblanceolate; aments appearing before or with the leaves, nearly unstalked or on short leafy stalks; capsules not or scarcely stalked; styles (0.5) 1 to 1.5 mm long; arctic or alpine.

Leafblades mostly 2 to 3.5 (5.5) cm long, 0.8 to 1.5 (2) cm wide, broadly pointed at tips, tapering to base; stipules none or soon falling; aments appearing mostly with the leaves, 1 to 3 (5) cm long; Rocky Mountains and Sierra Nevada. (*S. chlorophylla*) .....(Yl, RM) *S. planifolia*

Leafblades to 3.5 cm long, to 2 cm wide; aments nearly globose to short-cylindric, 1 to 3 cm long; styles to 1.5 mm long ..... (Yo, K, Yl, RM) var. *monica*

Leafblades to 5.5 cm long, to 1.5 cm wide; aments 1.5 to 5 cm long; styles 0.5 to 1 mm long ..... (Yl, RM) var. *nelsonii*

Leafblades generally larger, 3 to 6 (8) cm long, 1.5 to 3.5 cm wide, pointed at both ends; aments appearing mostly before the leaves, but sometimes not maturing until later, 2.5 to 7 cm long; styles 1 to 1.5 mm long; northwest.

Leafblades obovate, the veins conspicuously raised below; stipules lacking or soon falling ..... (MR) *S. pennata*

Leafblades rhombic or broadly oblanceolate; veins evident, but not as conspicuous as in the last; stipules long, narrow, persistent ..... (MK) *S. pulchra*

Commonly taller shrubs 1 to 5 m high, or small trees to 6 m high; buds slender; leafblades lanceolate or narrowly elliptic to narrowly oblanceolate (or linear), (2.5) 4 to 9 cm long, (0.3) 1 to 1.8 cm wide; stipules small, narrow, or none; aments appearing with the leaves, on short leafy stalks; capsules stalked; styles less than 1 mm long.

Pacific slope, common; low or tall shrubs; leafblades lanceolate to narrowly oblanceolate, to 9 cm long, 1 to 1.8 cm wide; fruiting aments 2 to 6 (7) cm long; capsules on stalks 0.5 to 2 (2.5) mm long.

Tall shrubs or small trees to 6 m high; twigs shiny dark reddish-brown; leafblades with gland-toothed margins, sometimes finely silky-hairy below; capsules on stalks 0.5 to 1.2 mm long; far north ..... (MK) *S. arbusculoides*

Low or tall shrubs 1 to 3 (5) m high; older twigs brown, the youngest often yellowish, thinly silky to glabrous; leafblades becoming glabrous, not toothed or few-toothed; capsules on stalks 1 to 2 mm long; southern Cascades and Sierra Nevada ..... (C, L, Yo, K, S) *S. lemmonii*

Rocky Mountains east of Continental Divide; shrubs generally less than 3 m high (in our area); leafblades linear to lanceolate, 2.5 to 7 cm long, 0.3 to 1.2 cm wide, silvery-silky or becoming glabrous, not toothed or obscurely so; aments 1 to 2 cm long; capsules on slender stalks 2.5 to 4 mm long; rare in our area ..... (RM) *S. petiolaris*

Leafblades more or less silky or woolly, at least below, at maturity, green and often shiny above; shrubs.

Shrubs 2 to 7 m high, found in parks of the northwest; aments appearing with the leaves, the staminate with stamens borne singly; capsules scarcely stalked; styles 0.5 to 0.7 mm long; leafblades elliptic to obovate or oblanceolate, 4 to 8 (10) cm long, 1.5 to 3 cm wide. Section SITCHENSES.

Leafblades obovate, tapering to narrow base, to 7 cm long, green and smooth above or hairy when young, white-satiny-hairy below; twigs mostly glabrous; stipules small, soon falling; scales brown, thinly hairy; anthers violet ..... (O, MR, C) *S. sitchensis*

Leafblades more elliptic to obovate, the base broader, to 8 (10) cm long, somewhat tough and leathery, dark green and nearly glabrous above, densely white-woolly below; twigs usually densely fuzzy or hairy; stipules 5 to 8 mm long; scales tawny, densely white woolly; anthers yellow ..... (O, MR, C) *S. coulteri*

Shrubs 0.2 to 4 m high, found in Rocky Mountains and California parks; aments appearing before or with the leaves, the staminate with stamens in two's; capsules stalked or not stalked; styles 1 mm long (or none); leafblades linear or oblong, lanceolate to oblanceolate, semi-ovate or obovate, 3 to 7 (10) cm long, (0.6) 1 to 3 (4) cm wide.

Leafblades thinnish, the margins not toothed, or sometimes wavy-scalloped, broadly oblong or oblong-lanceolate to oblanceolate or obovate, 3 to 7 (10) cm long, 1 to 3 (4) cm wide; scales pale to dark brown or black; styles evident; shrubs 1 to 4 m high. Section PELLITAE (Argenteae).

Twigs yellow to brown, glabrous, or finely hairy, without a white bloom; leafblades broadly oblong, elliptic, oval, or obovate, 3 to 6 (10) cm long, 1 to 3 (4) cm wide, green and finely hairy to glabrous above, lustrous below with dense shiny hairs, the midvein finely hairy; aments appearing before leaves, at ends of leafy branches; scales pale brown to brown; capsules silvery-silky, on stalks 0.5 to 1 mm long; styles 0.5 to 1 mm long .....(G) *S. drummondiana*

Twigs yellowish to brown or purplish-black, often with a whitish-bloom; leafblades oblong-lanceolate or oblanceolate, green above, densely white opaque-silvery-hairy below, the midvein glabrous; aments appearing with or before the leaves, short-stalked or sessile; scales brown to black; styles 1 to 1.5 mm long.

Leafblades 4 to 7 cm long, 1.5 to 2.5 (3.5) cm wide, somewhat rounded at base; aments appearing before the leaves, 3 to 6 cm long in fruit, short-stalked; scales black, densely woolly; capsules gray-silky, on stalks 1 mm long .....(G) var. *bella*

Leafblades 3 to 5 (7) cm long, 0.8 to 2.5 cm wide, pointed at both ends; aments appearing with the leaves; fruiting catkins 1 to 4 cm long, sessile or short-stalked; scales oblong to obovate, brown to black, thinly hairy; capsules scarcely stalked or on short stalks to 1 mm long .....(K, S, G, Yl, GT, RM, Z) var. *subcoerulea*

Leafblades thickish and often somewhat rugulose or wrinkled-looking above due to strongly impressed veins, the margins somewhat inrolled and often somewhat wavy-scalloped; scales pale brown; shrubs 0.2 to 1 (2) m high.

Leafblades linear to narrowly lanceolate or oblanceolate, 3 to 7 (10) cm long, 0.6 to 2 cm wide; stipules broadly lanceolate to semi-ovate, aments borne on short leafy stalks; capsules stalked; styles 0.7 to 1.5 mm long. Section CANDIDAE.

Shrubs 0.2 to 1 m high; young twigs white-woolly; leafblades densely white-woolly below, thinly so above; fruiting aments 1 to 3 cm long; capsules nearly sessile; styles 1 to 1.5 mm long, reddish; anthers purplish; bogs; northern Rocky Mountains east of the Divide .....(G) *S. candida*

Shrubs to 2 m high; young twigs finely hairy, becoming smooth and shiny; leafblades densely silky-hairy below, thinly silky above; fruiting aments to 5 (6) cm long; capsules on short stalks about 1 to 1.3 mm long; styles 0.7 to 1 mm long; anthers yellow; California parks, at high elevations .....(L, Yo, K, S) *S. jepsonii*

Leafblades roundish to elliptic or narrowly elliptic, 3 to 4.5 (6) cm long, 2 to 3.5 cm wide; stipules none; aments borne on slender naked stalks; capsules sessile; style none. Section RETICULATAE .....(G) *S. vestita*

b. *Ours low arctic or alpine plants with creeping or prostrate rooting stems and short erect or ascending branches mostly less than 20 cm high (except S. vestita); scales of catkins yellowish or dark brown to blackish.*

Leafblades thickish, elliptic or oval to roundish or broadly obovate, dark green above and often appearing wrinkled due to strongly impressed veins, whitish below, borne on slender petioles about ½ to nearly as long as the blade; aments linear, borne on naked stalks; scales yellowish to light brown, finely hairy or nearly glabrous; capsules finely woolly, sessile; styles very short or none. Section RETICULATAE.

More or less erect shrubs forming clumps to 1 m high; leafblades white-silky hairy below, especially on midrib and veins; petioles short, less than ¼ as long as

blade, stout; stalks of aments short, densely finely hairy; scales hairy; capsules to 5 (7) mm long; of limited distribution in western parks.

Leafblades broadly elliptic to roundish, 3 to 4 cm long, strongly wrinkled above due to impressed net veins; fruiting catkins 1 to 3 cm long .....(G) *S. vestita*

Leafblades narrowly elliptic, to 6 cm long, less strongly wrinkled above; fruiting catkins to 4 or 5 cm long .....(G) var. *erecta*

Creeping alpine plants, erect or with ascending branches (rarely more than about 15 cm high) from stout woody underground stems; leafblades glabrous or nearly so, on slender petioles mostly ½ to as long as the blades; flowering stalks naked, nearly glabrous or hairy, ½ to as long as aments; capsules 2.5 to 3 (4) mm long; some species widespread.

Stalks of aments more or less hairy; scales mostly hairy, at least on inside; far north.

Leafblades 1 to 3 cm long; fruiting aments 2 to 4 cm long.

Leafblades elliptic to oval or obovate .....(MK) *S. reticulata*

Leafblades oval to roundish or broadly obovate .....(MK) var. *subrotunda*

Leafblades 4 to 6 cm long, broadly obovate to roundish; fruiting aments to 5 (6) cm long .....(MK) var. *gigantifolia*

Stalks of aments mostly nearly glabrous, the scales glabrous; Rocky Mountains and northwest.

Leafblades 1 cm or less long; catkins few-flowered .....(O, MR, Yo, G, Yl, RM) *S. nivalis*

Leafblades 1 to 3 cm long; catkins several-flowered .....(G, Yl, GT, RM) var. *saximontana*

Leafblades thinnish, oblong or elliptic to oval, roundish, or narrowly obovate, not strongly impressed-veined above, green on both sides, often paler below, borne on relatively short petioles mostly less than ½ as long as the blade (except sometimes in *S. arctica*); aments rather stout, or very small and few-flowered, borne on leafy stalks; scales light to dark brown or blackish; capsules very short-stalked or sessile; styles evident, 0.5 to 1 (1.5) mm long.

Closely matted herb-like plants with slender branching underground stems and short ascending branches not usually exceeding 5 cm; old dried leaves often more or less persistent; leafblades flat, mostly less than 2 cm long (or to 6 cm in *S. setchelliana*); scales pale yellow or brownish to black, more or less hairy to nearly glabrous; capsules finely hairy to nearly glabrous; not common in western parks. Section RETUSAE.

Leafblades 2 to 5 (6) cm long, nearly sessile, yellowish-green on both sides, narrowly to broadly oblanceolate or obovate, at first somewhat hairy, becoming glabrous except on midrib and main veins below, the margins more or less gland-toothed; young twigs usually white-hairy, becoming glabrous; scales glabrous, pale yellow or straw-color; capsules glabrous; far north .....(MK) *S. setchelliana*

Leafblades mostly less than 2 cm long, rarely more than 1.5 cm, distinctly petioled, green on both sides or paler below, glabrous or sometimes with marginal fringe of hairs, entire or nearly so; twigs glabrous or thinly hairy; scales glabrous to more or less densely hairy-fringed.

Ascending stems to about 5 cm high; leafblades bright green above, paler below, 0.8 to 2 (2.5) cm long, more or less pointed at both ends; aments 0.5 to 2 (4.5) cm long; scales brown to blackish; capsules 4 to 5 (6) mm long; styles 0.7 to 1.5 mm long.

Leafblades narrowly elliptic to narrowly obovate, 0.8 to 1.5 cm long; old leaves somewhat persistent on stems; capsules finely gray-hairy, not stalked; styles 1 to 1.5 mm long; northern Rockies and northwest (*S. tenera*) .....(MR, G, Yl, GT, RM) *S. cascadensis*

Leafblades mostly obovate, 1 to 2 (2.5) cm long; old leaves not persistent; capsules becoming glabrous, or thinly hairy at tips, on short stalks 0.5 to 1 mm long; styles to 1 mm long; far north .....(MK) *S. polaris* and var. *selwynensis*

Ascending stems scarcely more than 2 cm high; old leaves more or less persistent; leafblades green on both sides, 0.4 to 0.8 (1) cm long, rounded or pointed; aments tiny, few-flowered; scales light brown; capsules to about 3 mm long; styles short, but usually evident.

Leafblades oval or elliptic to roundish, mostly rounded at both ends (or notched at tips); scales nearly glabrous, capsules glabrous .....(MK) *S. rotundifolia*

Leafblades oval or elliptic to oblong, more or less pointed at both ends; scales with long-hairy fringe at least at tip; capsules somewhat constricted above, more or less hairy.

Aments several-flowered; old leaves strongly persistent; far north .....(MK) *S. phlebophylla*

Aments few-flowered; leaves more or less persistent; rare in Rocky Mountains .....(Yl, GT) *S. dodgeana*

Mostly openly spreading plants with stout, distinctly woody prostrate stems spreading somewhat above ground; ascending branches becoming 10 to 20 cm long; old dried leaves not persistent; leafblades 1.5 to 5 (6) cm long, often folded at tips; scales dark brown to blackish, at least at tips, long-hairy at least near tips, sometimes nearly glabrous below on the outside; capsules whitish- or gray-woolly; widespread. Section OVALIFOLIAE (Arcticae, in part).

Leafblades 2.5 to 5 (6) cm long, 1 to 2.5 (3.5) cm wide, elliptic-oval to narrowly obovate, more or less hairy when young, becoming glabrous; aments densely flowered, 3 to 6 (10) cm long, 1 to 1.8 cm wide; far north.

Petioles 0.9 to 2 cm long; stipules narrowly ovate to lanceolate, 0.2 to 1.2 cm long .....(MK) *S. arctica*

Petioles not exceeding 1 cm long; stipules smaller or none .....(MK, G) *S. anglorum*

Leafblades generally smaller, 1.5 to 3.5 (4.5) cm long; more or less hairy, at least when young; aments shorter, 1 to 2.5 (3.5) cm long, on somewhat shorter stalks; Sierra Nevada and Rocky Mountains .....*S. anglorum* vars.

Leafblades broadly elliptic to roundish or obovate, 1.2 to 2.5 (3) cm wide, short-pointed or rounded at tips; branchlets stout; aments densely-flowered .....(G) var. *kophophylla*

Leafblades elliptic-oblong or elliptic-oval to broadly oblanceolate; branchlets more slender; aments often more distantly flowered at base.

Branchlets to 20 cm long, sometimes covered with a white bloom, soon becoming glabrous; leafblades thinnish, elliptic-oval to narrowly obovate, 1 to 2 (2.5) cm wide, mostly rounded or blunt-pointed at tip, becoming glabrous .....(G) var. *araioclada*

Branchlets generally shorter, to 10 cm long, somewhat hairy when young; leafblades firm, elliptic-oblong to broadly oblanceolate, 0.7 to 1.5 (1.8) cm wide, usually pointed at tips.

Leafblades becoming glabrous; Rocky Mountains (*S. petrophila*) .....(G, Yl, GT, RM) var. *antiplasta*

Leafblades at maturity gray-hairy above; Sierra Nevada .....(L, Yo, K, S) forma *caespitosa*

OCCURRENCE.—*Salix alaxensis:* MK; var. *longistylis:* MK; *amygdaloides:* G; *anglorum:* MK; var. *antiplasta* (*S. petrophila*): G, Yl, GT, RM; forma *caespitosa:* L, Yo, K, S; var. *araioclada:* G; var. *kophophylla:* G; *arbusculoides:* MK; *arctica:* MK; *barclayi:* MK, O, MR, G, Yl, RM; *barrattiana:* MK; var. *angustifolia:* MK; var. *tweedyi* (see *S. tweedyi*); *bebbiana:* MK, G, Yl, RM, Z, GC; var. *perrostrata:* MK, G,

Yl, RM; *bella* (see *S. drummondiana* var.); *brachycarpa* (*S. stricta*): G, Yl, GT, RM; var. *mexiae:* MK; *candida:* G; *cascadensis* (*S. tenera*): MR, G, Yl, GT, RM; *caudata:* G, Z; var. *bryantiana:* G, Yl, GT, RM; var. *parvifolia:* G, Yl, GT; *chlorophylla* (see *S. planifolia,* and *S. subcoerulea* as to Rocky Mountain parks); *commutata:* O, MR, G; *cordata* (see *S. mackenziana*); *coulteri:* O, MR, C; *desertorum:* Yl, GT, RM; *dodgeana:* Yl, GT; *drummondiana:* G; var. *bella:* G; var. *subcoerulea* (*S. chlorophylla,* in part): K, S, G, Yl, GT, RM, Z; *eastwoodiae:* C, Yo, K, S; *exigua:* Yl, RM, MV, B, Z, GC; var. *nevadensis:* K; var. *stenophylla:* RM, B; var. *virens:* Yo, S; *farrae:* G, Yl; *fendleriana* (see *S. lasiandra*); *geyeriana:* G, Yl, GT, RM, Z; var. *argentea:* Yo, K, S, Yl, RM; var. *meleina:* MR; *glauca* var. *acutifolia:* MK; var. *aliceae:* MK; var. *glabrescens:* MK (see *S. pseudolapponum* as to Rocky Mountain forms); *glaucops* (see *S. pseudolapponum*); *gooddingii* (*S. nigra* var. *vallicola*): Yo, S, Z, GC; *hindsiana:* C, Yo, S; *interior:* G; *irrorata:* RM; *jepsonii:* L, Yo, K, S; *laevigata:* Yo, Z; (var. *araquipa:* Yo, GC; *lasiandra:* O, MR, K, S, Yl, B; var. *abramsii:* C, Yo; var. *lancifolia:* O, MR, K, S; *lasiolepis:* MR, Yo, S, Z; *lemmonii:* C, L, Yo, K, S; *lutea* (*S. watsonii*): MR, GT, RM, B, Z; var. *ligulifolia:* Yo, S, GC; *mackenziana* (*S. cordata* var.): MR, Yo, S, G, Yl; *melanopsis:* Yo, K, S, G, Yl; var. *bolanderiana:* Yo, G; var. *tenerrima:* S, G; *monica* (see *S. planifolia* var.); *monochroma:* G, Yl; *monticola:* RM; *myrtillifolia* (*S. pseudomyrsinites,* in part): MK, G, Yl, RM; *niphoclada:* MK; *nivalis:* O, MR, Yo, G, Yl, RM; var. *saximontana:* G, Yl, GT, RM; *orestera:* C, Yo, K, S; *pennata:* MR; *petiolaris:* RM; *petrophila* (see *S. anglorum* var. *antiplasta*); *phlebophylla:* MK; *piperi:* O, MR; *planifolia:* Yl, RM; var. *monica:* Yo, K, Yl, RM; var. *nelsonii:* Yl, RM; *polaris:* MK; var. *selwynensis:* MK; *pseudocordata* (*S. pseudomyrsinites,* in part): MK, C, L, Yo, K, S, G, RM; *pseudolapponum* (*S. glaucops* and *S. glauca* var. *glabrescens* as to Rocky Mountain forms): G, Yl, GT, RM; *pseudomonticola:* G, Yl, RM; var. *padophylla:* RM; *pseudomyrsinites* (see *S. myrtillifolia* and *S. pseudocordata*); *pulchra:* MK; *reticulata:* MK; var. *gigantifolia:* MK; var. *subrotunda:* MK; *richardsonii:* MK; *rotundifolia:* MK; *saximontana* (see *S. nivalis* var.); *scouleriana:* O, MR, C, Yo, K, S, G, Yl, GT, RM, Z, GC; var. *coetanea:* L; *serissima:* G, RM; *setchelliana:* MK; *sitchensis:* O, MR, C; *stricta* (see *S. brachycarpa*); *subcoerulea* (see *S. drummondiana* var.); *taxifolia:* Z, GC; *tenera* (see *S. cascadensis*); *torulosa* (see *S. anglorum* and *S. arctica* as to MK; *tweedyi* (*S. barrattiana* var.): G, Yl, GT; *vestita:* G; var. *erecta:* G; *walpolei:* MK; *watsonii* (see *S. lutea*); *wolfii:* RM; var. *idahoensis:* Yl, GT.

On Homoeosis, as Well as Other Aberrations, and Their Origin in an Earthworm Species, Eisenia foetida (Savigny, 1826), Along with Some Deductions as to Morphogenesis in the Lumbricidae[1]

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Homoeosis in *E. foetida*, when symmetrical and not involved in metameric abnormality, has been thought (Gates, 1949) to have a postembryonic origin, anterior and posterior homoeosis resulting respectively from hypo- and hypermeric head regeneration. However, an aberration in embryonic development that is believed to be responsible for the recently recorded asymmetry in a biclitellate specimen (Gates, 1956b) occasionally ought to result in symmetrical homoeosis.

Further study of the subject has been permitted by a collection obtained early in November, 1956, the results of which are presented herewith along with a report on the internal anatomy of the biclitellate worm.

Material

All worms considered below, except the biclitellate specimen and three others, were obtained in a single collection from one small section of a cow-manure pile at Orrington, Maine. Anomalies of metamerism, split (or compound) metameres and helicometameres (or spirals), are common. Fifty-two of the 232 worms have one or more in a region between the peristomium and intersegmental furrow 33/34, an incidence of more than 22 percent. Ten of those 52 have two discrete anomalies in the above-mentioned region, three have three anomalies (several segments apart in each case), the remainder (39 specimens) only one. Each segmental level from ii to xxxiii has been involved in abnormal metamerism. The number of times a particular segment is included rises gradually to a peak at xxx-xxxii (each of those 15 or more times). Abnormality of metamerism is present in the first 9 segments 5 times, in the region comprising x-xix 16 times, in xx-xxv 19 times, in xxvi-xxxii 28 times (an anomaly extending into two of the regions just mentioned being referred only to that in which its major portion is contained.) Additional abnormalities often are present posteriorly (but will not be considered further) and a number of those with normal metamerism in front of 33/34 have one or more aberrations posteriorly.

Results

Homoeosis is externally indicated, in the Orrington series, only by genital apertures. Metamerism may or may not be abnormal in or anterior to the

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homoeotic region. Homoeosis, uncomplicated by aberrant metamerism in the first 15 segments, characterizes 22 of the 232 worms. Actual incidence may have been somewhat nearer to ten percent as 9 of the juveniles are too young for evidence of organ dislocations to be recognizable externally. Six of the 22 homoeotics have metameric anomalies in the region between the male-pore segment and 33/34, one of the six with three anomalies between xvii and xxxii. Some of the homoeotics have one or more abnormalities in metamerism behind 33/34.

HOMOEOSIS UNCOMPLICATED BY METAMERIC ABNORMALITY

Locations of genital apertures and of important reproductive organs, in the 22 homoeotic specimens, are shown in Table I. Hearts, when present in xii, also are indicated.

One specimen (No. 1, Table I) differs from normal by having every organ from the first pair of hearts (which should be in vii) to the gizzard (which should be in xvii), on each side of the body, one segment behind the usual location. Simultaneous translocation of so many organs, in one individual, is contraindicated by one's knowledge of mutation and earthworm phylogeny. An extra segment, then, must have been intercalated in front of vii. Such intercalation could have resulted from production of one more metamere than had been amputated, during development of a new head, as cephalic regeneration has been shown (Gates, 1949), in *E. foetida,* occasionally to be hypermeric. The usual external stigmata of regeneration are quite unrecognizable in No. 1 but they disappear shortly in case of head regenerates. No indications of cephalic regeneration were recognized in the rest of the Orrington series though six worms do have tail regenerates. Halving of one mesoblastic somite on each side of the embryo (Gates, 1956 a-b), anterior to the seventh level, also could have produced the homoeosis. Although an embryonic, as well as a post-embryonic origin of the homoeosis in specimen No. 1 now seems possible, criteria for distinguishing one from the other are at present unknown.

Organ homoeosis of the sorts shown by specimens numbered 2-22, regardless of regeneration, must have had an embryonic origin.

Specimens 2-4

The unilateral homoeosis in these worms requires posterior translocation of ovary, oviduct, and ovisac as well as of male terminalia on the right side, or, intercalation on the right side only of one segment between the last testis metamere and that containing the ovary. Translocation of male terminalia, anteriorly as well as posteriorly, in an occasional mutant individual, is known but no such shift of gonads has been recognized. The intercalation apparently required by these three worms can have resulted only from halving of the right mesoblastic somite at the twelfth level.

Specimen No. 4 is juvenile, possibly too young for spermathecae and anterior seminal vesicles to have been recognizable in a dissection. Intestinal origin is in xvi on both sides, though to be expected in xv on the left side. The gizzard is asymmetrical, mostly in xviii on the right side, mostly in xvii on the left side, the circular muscle fibres somewhat diagonal rather than transverse to the long axis of the body.

Specimens 5-10

Mutational organ translocation has the same contraindications in this as in the previous group and would not explain unilateral duplication of ovary, oviduct and ovisac. Intercalation by mesoblastic halving, however, simultaneously explains organ duplications since daughter half-somites, if separated from each other early enough, retain (cf. Gates, 1956a-b, 1957) all developmental potentialities of the parent block. Accordingly, the intercalation here required must have resulted from halving of a mesoblastic

TABLE I.—Homoeosis in *E. foetida*

Serial number	Spermathecal pores on intersegmental furrows	Female pores in segments		Male pores in segments		Testes and male funnels in segments			Seminal vesicles in segments					Ovaries and oviducal funnels in segments		Hearts in segment
		14	15	15	16	10	11	12	9	10	11	12	13	13	14	12
		L R	L R	L R	L R	L R	L R	L R	L R	L R	L R	L R	L R	L R	L R	L R
N		* *	– –	* *	– –	* *	* *	– –	* *	* *	* *	* *	– –	* *	– –	– –
1	10/11-11/12	– –	* *	– –	* *	– –	* *	* *	– –	* *	* *	* *	* *	– –	* *	* *
2-3		* –	– *	* –	– *	* *	* *	– –	* *	* *	* *	* *	– –	* –	– *	– –
4	0	* –	– *	* –	– *	* *	* *	– –	– –	– –	* *	* *	– –	* –	– *	– –
5-7		* *	– *	* –	– *	* *	* *	– –	* *	* *	* *	* *	– –	* *	– *	– –
8		* *	– *	* –	– *	* *	* *	– –	– –	– –	* *	* *	– –	* *	– *	– –
9		* *	* –	– *	* –	* *	* *	– –	* *	* *	* *	* *	– –	* *	* –	– –
10		– *	* –	– *	* –	* *	* *	– –	– –	– –	* *	* *	– –	× *	* –	– –
11	?	– *	* –	– *	* –	– *	* *	* –	– –	* *	* *	* *	* –	– *	* –	* –
12	0	* –	– *	* –	– *	* –	* *	* –	– –	– –	* –	* *	– *	– *	– *	– *
13-14	L 11/12	– *	* –	– *	– *	* *	* *	* –	* *	* *	* *	* *	* –	– *	* –	* –
15-16	11/12	– –	* *	– –	* *	* *	* *	* *	* *	* *	* *	* *	* *	– –	* *	* *
17	11/12	– –	* *	– –	* *	* *	* *	* *	– –	– –	* *	* *	* *	– –	* *	* *
18	L 11/12	– –	* *	– –	* *	* *	* *	* –	* *	* –	* *	* *	* –	– –	* *	* –
19	L 11/12	– *	* *	– –	* *	* *	* *	* –	– –	– –	* *	* *	* –	– *	* *	* –
20	0	– –	* *	– –	* *	– *	* *	* –	– *	* *	* *	* *	* –	– –	* *	? –
21	L 11/12	– –	* *	– –	* *	– *	* *	* –	– *	* *	* *	* *	* –	– –	* *	* –
22	11/12	* *	– –	* –	– *	* *	* *	* *	* *	* *	* *	* *	* *	– –	* *	* *
31	L 11/12	* –	– *	* –	– *	* *	* *	– *	* –	* *	* *	* *	– *	* –	– *	– *

L Left side
R Right side
* Present
– Absent
N Normal
× Ovary present, as well as its sac, but no female funnel.

Spermathecal pores are present in 9/10-10/11 unless otherwise indicated in the table or in the text.

Segments are indicated, at heads of columns, by Arabic instead of Roman numerals for greater convenience.

An ovisac is present, in proper position, behind each ovary. Hence, ovisacs are omitted from the table.

somite at the thirteenth level, on the right side of Nos. 5-8, on the left side of Nos. 9-10.

The ovary on the left side of xiii, in No. 10, as well as the ovisac on the left side of xiv, is rudimentary and there is no oviducal funnel on the left side of xiii. The ovary on the left side of xiv is normal and with the usual egg string. The posterior ovisac on right side, of Nos. 5 and 6, is evaginated into xiv.

Intestinal origin is in xv on both sides in No. 6, in xvi on both sides in Nos. 9 and 10, in xv on the left side but in xvi on the right side of Nos. 5, 7, 8. The gizzard is mostly in xvii in Nos. 5 and 6, mostly in xviii in Nos. 8 and 9, is asymmetrical in Nos. 7 and 10 and there mostly in xvii on the left side but mostly in xviii on the right side.

Specimens 11-12

The intercalations here required could have originated by halving of one embryonic somite, on the left side in No. 11 and on the right side in No. 12, at some level anterior to the tenth.

Intestinal origin is not determinable but the gizzard is mostly in xviii. The athecal specimen is juvenile. Locations of spermathecal pores and of the spermathecae could not be determined in No. 11 but those on the right side probably were in the usual positions, those of the left side more posteriorly by one level.

Specimens 13-14

The intercalation in these worms could have arisen by halving, on the left side, of one somite, either at the tenth or at the eleventh level.

Intestinal origin is in xvi. The gizzard is asymmetrical but is mostly in xviii. Spermathecae, in No. 13, are present only in ix, with pores at 9/10. Absence of other spermathecae is not explained by somite halving.

Specimens 15-16

The symmetrical homoeosis in these worms requires halving of one mesoblastic somite on each side. The reproductive organs and the hearts show that the splitting was at the tenth or eleventh level. Condition does not permit more exact specification but in these two cases symmetrical homoeosis apparently could have originated from somite halving at tenth level on one side and at the eleventh level on the other side.

Intestinal origin is in xvi in both worms. The gizzard, in No. 15, is in xvii but in No. 16 is in xviii and an anterior portion of xix. Presence of the gizzard in xvii is not explained by somite halving.

Specimen 17

The calciferous gland, in this worm, begins in xii, which requires the intercalation to have arisen from splitting of both mesoblastic somites at the tenth level.

Absence of seminal vesicles in ix-x is not explained by somite splitting.

Presence of sperm in the spermathecae, including the extra ones, shows that the worm, like some of the other homoeotics, had been able to copulate in spite of the abnormality. Iridescence on the male funnels, as well as in some other homoeotics, shows that sperm had been matured.

Specimen 18

Although the homoeosis in this worm appears externally to be symmetrical (and as to be expected in hypermeric regeneration) the internal anatomy is asymmetrical. The intercalations require halving of the somite at the twelfth level on the right side, and of one somite at the tenth or at the eleventh level on the left side. In spite of that difference, metamerism is normal externally as well as internally (insofar as septa, excretory and nervous systems are concerned).

The gizzard appears to be mostly in xvii, a location that is not explained by somite halving. Intestinal origin is not determinable. Seminal vesicles are rudimentary in ix, quite small in x.

Specimen 19

Although the male pores are displaced symmetrically, the bilateral difference in number of female pores indicates intercalation probably can be expected at different levels. The internal anatomy shows that the levels at which somites were split are the thirteenth on the right side and either the tenth or the eleventh on the left side.

Intestinal origin is in xvi and the gizzard is in xviii.

Specimens 20-21

The intercalations evidenced by these worms originated, in each specimen, by halving of a mesoblastic somite anterior to the tenth level on the left side and of the somite at the twelfth level on the right side. Nevertheless, metamerism, anterior to 33/34, is normal both externally and internally.

The intestinal origin is in xvi and the gizzard is in xviii as is to be expected from the somite splitting. Specimen No. 20 is juvenile, perhaps too young for spermathecae to be recognizable.

Somite halving has accounted for all of the organ homoeosis in some of the worms considered above and in previous contributions (Gates, 1956a-b) and for most of it in others. Occasional organ deficiencies and a small portion of the organ homoeosis require other explanation. For the deviation from expected homoeotic location of the gizzard as instanced above, a "regularization" (Gates, 1957) seems to be responsible. That process also appears to have resulted in some of the deviation from anticipated location of the intestinal origin.

Specimen 22

The intercalation here required, according to evidence provided by the testes, seminal vesicles and spermathecae, could have resulted from splitting of mesoblastic somites at either the tenth or eleventh levels. Calciferous lamellae are lacking in x-xi, the gland definitely beginning in xii, which suggests that the tenth level is the one involved on each side.

Intestinal origin is in xvi and the gizzard is in xviii, as is to be expected from the intercalation.

The somite halving apparently required by the anterior reproductive organs and the calciferous gland does not explain location of left ovary, oviduct and ovisac, of left male terminalia, nor the location of the female pore on the right side. Opening of an oviduct externally in the segment that contains

its own funnel appears not to have been recorded in the Lumbricidae hitherto and must be a very rare aberration.

Only elimination of the left somite at the twelfth level will provide a single explanation of location of the left ovary and of the left male and female terminalia. Although that elision could have put intestinal origin in xv and gizzard in xvii, on the left side, regularization presumably could have resulted in the observed symmetry.

The homoeosis in the above-considered 22 specimens, if embryonic origin in No. 1 is assumed, requires elision of one mesoblastic somite and splitting of thirty-one. Twin daughter-somites were, in each instance, completely separated from each other. Twin daughter-somites, in each case, must have been halves unless they had capacity otherwise to become equisized. Parent somites must have been split into anteroposterior portions unless daughter blocks subsequently were rearranged into anteroposterior sequence.

One somite was split in thirteen specimens, two somites in nine specimens and then at the same level on both sides in two (possibly one to three more) but at different levels on opposite sides in four (possibly one to three more) specimens. A somite was split at one of the eight levels anterior to x, at the tenth and/or eleventh level, at the twelfth level, at the thirteenth level, respectively, on six, twelve, six and seven occasions. Subsequent development, in each worm, enabled normal metamerism both externally and internally except for septal insertions on a short anterior portion of the intestine where regularization of asymmetry seems to take place.

Other Orrington worms, with all female and male pores in normal equatorial position and with the pores of one side behind those of the other side appear to be homoeotic. However, all organs of both sides are in their normal segmental location along the anteroposterior axis. This "apparently but not really" (Shorter Oxford English Dictionary) homoeotic condition can be appropriately termed "pseudo."

PSEUDOHOMOEOSIS

This condition, which characterizes five of the Orrington worms in each of which it could not have resulted from regeneration, must have originated early in embryonic development.

Specimen 23

The twelfth segment on the right side splits at mD and mV into two metameres (xii-xiii) on the left side, intersegmental furrow 11/12 on the left side ending blindly near mD and mV. Segments xii-xiii of the left side are half the size of adjacent metameres but are otherwise normal as each has a nephropore and four setae in the usual positions. No further abnormality in metamerism is recognizable externally until xlii.

Septum 12/13 of the left side ends mesially at the gut but 13/14 is continuous mesially with right septum 12/13. Intestinal origin is in xv on the right side and in xvi on the left side but the gizzard is in xvii. Septal insertions on the intestine from 17/18 anteriorly are abnormal.

Although "split" adequately characterizes appearances, both externally and internally, the reproductive organs and the hearts are so located as to require an abnormal median union of mesoblastic somites to have taken place.

The somites at the twelfth and thirteenth levels on the left side, in this specimen, united mesially with the twelfth somite of the right side, both dorsally and ventrally.

Specimen 24

Mesoblastic somites at tenth and eleventh levels on the right side had united mesially, both dorsally and ventrally, with the left somite at the tenth level. No further abnormality in metamerism is recognizable externally until xlii of the left side is split into two on the right side.

The intestinal origin is in xv on the left side and in xvi on the right side but the gizzard is in xvii. Insertions of septa 16/17-15/16 on the gut are abnormal. The dorsal blood vessel is doubled through one segment just behind the region of abnormal metamerism.

Specimen 25

Mesoblastic somites at tenth and eleventh levels on the right side had united mesially, both dorsally and ventrally, with the left somite at the tenth level. Segment xxii of the right side is split into two on the left side and xl-xli of the right side are united on the left side.

The right coelomic cavity of xi is smaller than that of x (and the seminal vesicle therein is almost rudimentary) though no difference in size of x and xi on the left side is externally recognizable. The intestinal origin is in xv on the right side and in xvi on the left side. The gizzard is in xvii on the left side and in xviii on the right side. Insertions of septa 16/17-17/18 on the gut are abnormal.

Specimen 26

Mesoblastic somites at thirteenth and fourteenth levels on the right side had united mesially, both dorsally and ventrally, with the left somite at the thirteenth level. The twenty-first segment on the left side splits into two halves on the right side.

Specimen 27

Mesoblastic somites at fourteenth and fifteenth levels on the right side had united mesially, both dorsally and ventrally, with the left somite at the fourteenth level. No further anomalies in external metamerism (as also in case of Nos. 26 and 28) are recognizable until behind the clitellum.

Mesoblastic somites at fifteenth and sixteenth levels on left side of No. 28, which probably should not be called pseudohomoeotic, had united mesially, both dorsally and ventrally, with the right somite at fifteenth level. Septal insertions on the anterior portion of the intestine, in this worm also, are abnormal.

A normal segment or metamere, in earthworms, originates during embryogenesis by symmetrical median union, both dorsally and ventrally, of two mesoblastic somites. An abnormal segment or metamere that arises by median fusion of three somites is, then, preferably characterized as compound rather than split, in spite of appearances. Compound metameres, of the same sort as in specimens 23-28, are present, in the Orrington worms, at various levels back almost to the anal region. Other abnormal metamerism, in the Orrington worms, is of the spiral kind. The helicometamere, like the compound segment must arise when a mesoblastic somite of one side unites mesially

with two somites of the opposite side. The difference from the compound metamere is a result of dorso-ventral asymmetry in the union. The somite at the fourteenth level in No. 29 (right side) and 30 (left side) had united ventrally with the somite at the fourteenth level of the opposite side, but dorsally had united with the somite at the fifteenth level. No splitting of mesoblastic somites had been involved in Nos. 29-30 nor in other specimens that are omitted from further consideration.

UNILATERAL HOMOEOSIS ASSOCIATED WITH SPIRAL METAMERISM

One illustration of that combination of aberrations is provided by specimen No. 31. The external characteristics and internal anatomy of this worm are such (*cf.* Table I) as to require intercalation of one segment by halving of the mesoblastic somite at the eleventh level on the right side. The posterior daughter-somite, which may be conveniently designated as R11b, had united dorsally with two somites, those at the twelfth and thirteenth levels on the left side, but ventrally with the one at the twelfth level on the left side. The spiral thus begun ends in front of 15/16.

The intestinal origin is in xv on the left side and in xvi on the right side but the gizzard is in xvii.

OTHER ABNORMALITY

No male pore, tumescence or cleft could be found, in No. 32, on the right side. The right male deferent ducts attenuate behind septum 12/13 and disappear before reaching xv. Metamerism is normal back to xix where a spiral (or series of them) begins. Metamerism becomes normal again only at xxv.

HOMOEOSIS IN A BICLITELLATE SPECIMEN

The explanation of the origin of the biclitellate condition in this specimen of *E. foetida* (Gates, 1956b), was based on external characters alone. The internal anatomy, now studied in dissection, supports the previous deductions.

External characteristics not previously mentioned are as follows: A male tumescence with the usual slight cleft but no male pore, on right side of xxvii. Female pores of right side on xxiii-xxiv, the posterior pore between *a* and *b* rather than lateral to *B*.

Metamerism, as previously noted, is normal back to 10/11. Metameric anomalies are of two sorts: Compound metameres such as the following Rx+Rxi/Lx, Rxii+Rxiii/Lxi. Spirals, of which the following is an example: Rxiv, Rxv and Rxvi united ventrally with Lxii but dorsally only the first two united with Lxii, Rxvi continuous dorsally with Lxiii and included in a spiral which terminates just beyond mV in xiv (as counted on the left side).

Internal anatomy.—Left side. Hearts, in vii-xii. Spermathecae, on anterior faces of 10/11-11/12. Testes and male funnels, in xi-xii. Seminal vesicles in x, xii, xiii. Ovary and oviducal funnel, in xiv. Ovisac, in xv. Intestinal origin, in xvi. Gizzard, in xviii-xx.

Right side. Hearts, in x-xix. Spermathecae on anterior faces of 15/16-18/19. Testes and male funnels, in xvi-xix. Seminal vesicles, only in xv, xvii, xx. Ovaries and oviducal funnels, in xxii-xxiii. Ovisacs, in xxiii-xxiv. Intestinal origin, in xxv. Gizzard, in xxviii. (Anterior and posterior boundaries of calciferous gland not identifiable on either side. Typhlosole begins behind xxviii.)

The gizzard, in a dissection from the dorsal side that destroyed upper halves of the septa, was not distinguishable externally from adjacent whitened portions of the intestine. Removal of a dorsal portion of the gut showed that the marked thickening of the circular muscle layer that constitutes the gizzard is located, in the ventral half of the body (spiral metamerisms involved here) as stated above. None of the circular muscle fibres in the gizzard is transverse to the long axis of the body. All are markedly diagonal, passing from xxviii anterolaterally into xviii-xx.

Although maturity is indicated by maximal tumescence of the clitellum and possibly also by the egg strings of the ovaries, sperm apparently had not been matured. All seminal vesicles are small though perhaps not rudimentary. The worm may have been male sterile. Spermathecal ampullae are quite empty but there are no spermatophores externally to indicate that copulation had been attempted.

The reproductive and circulatory systems require intercalation of segments by halving the mesoblastic somite at the seventh level on the left side, and, on the right side, by halving each somite at seventh to fifteenth levels as well as at three levels in front of the seventh (assumed to be the fourth to sixth). Those intercalations, would however result, unless there is some subsequent modification of development, in a half-gizzard in the right side of xxix (or posteriorly) and another half-gizzard in the left side of xviii. Presumptive half-gizzards during embryogenesis, judging from conditions in this adult, must have been so strongly attracted toward each other as to result in median union in spite of the disparity in levels. Such regularization is supported also by conditions in aberrant individuals of various earthworm species where half-gizzards never have been found. Regularization of the gizzard seems likely to ensue further modifications in development that can be expected to account for most of the aberrant structure in adjacent regions that is unexplained by somite splitting.

Except for the gizzard, then, structure on one side of the body of an earthworm can be considerably modified during development without entailing macroscopically recognizable change on the opposite side. The asymmetry of intercalations in the biclitellate worm provides an especially good illustration of a monolateral limitation on inductive capacity of the gonads. That capacity can be stated as follows. A testis induces development of a male funnel with deferent duct and of seminal vesicles only on its own side of the body and only from its own septum and/or that next behind. An ovary induces development of an ovisac and of an oviducal funnel with oviduct only on its own side of the body and only on the septum next behind. Because of that limitation a seminal vesicle should not be expected in the posterior of the two segments derived by splitting of the somite at the twelfth level in the biclitellate as well as monoclitellate homoeotics (cf. Nos. 2-4, 18, 20, 21). Absence of seminal vesicles, in certain circumstances, does not, then, raise any question as to retention of parent potentiality by daughter somites.

Normal segment size, in the biclitellate specimen, had resulted from symmetrical median union of the following mesoblastic somites: R4a with L4, R4b with L5, R5a with L6a, R5b with L6b, R6a with L7, R6b with L8.

In spirals, except at the ends, segments are of normal size, whether resulting from mesial union of half somites with half somites or unhalved somites.

HOMOEOSIS OF MIXED ORIGIN

Somite splitting, as already noted above, cannot explain all of the homoeosis in specimen No. 22, some of the organ locations requiring elimination of a somite on one side of the body behind the region of splitting. Whether such elision results from fusion with an adjacent somite on its own side of the body or from total regression, developmental potentiality was aborted.

ANTERIOR, ASYMMETRICAL HOMOEOSIS UNCOMPLICATED BY ABNORMAL METAMERISM

Records for several thousand specimens of *E. foetida* examined by the author during the last fifteen years have been searched for instances of homoeosis that might require somite abortion. The only homoeotics in a series of 472 clitellate worms from Darjiling, do have all reproductive organs and the last heart, on the left side in one and on the right side in the other, one segment in front of normal location. The homoeosis must have had an embryonic orgin. Unfortunately, however, no evidence was found that would show which side actually is homoeotic. A double origin of the aberrant conditions, accordingly, seems preferable, especially in view of the presence of one head (with normal metamerism) and many tail regenerates in the same collection. Halving of one embryonic somite at some level anterior to x, then produced the original homoeosis which was posterior. Subsequently, after hatching presumably, and following anterior amputation, there was regenerated a head having one segment less than had been lost.

A double origin for the observed homoeosis also seems to be required by a specimen of *E. foetida* from another American locality. Segmental intercalations in this worm (numbered 33 for convenient reference) require doubling of each somite at the thirteenth level. The intestinal origin in xvi as well as the location of the gizzard symmetrically in xviii and an anterior portion of xix also require splitting at the thirteenth level. The male terminalia of the right side, however, are not in xvi where they should be but in xv along with the posterior female pore. Somite abortion which was invoked in the case of No. 22 is definitely contraindicated in the present instance. The difficulty is resolved if, prior to embryogenesis, development of the right male terminalia in xiv (but now xv because of the intercalation) already had been determined.

Specimens with homoeosis restricted to the male terminalia have not been recognized, during the last fifteen years, in any of the collections of *E. foetida*. In various species of other lumbricid genera, male terminalia occasionally have been found, anterior or posterior to the usual locations on one or both sides of the body, in individuals where other organs, including clitellum and tubercula pubertatis, deny possibility of segment intercalation and deletion. Homoeotic terminalia, in each case, are normally positioned

with reference to meridians of longitude and the equator of the segment. Potentiality for development of the terminalia is, then, transferable from one somite to the next, in either direction, and independently on each side. Such mutant homoeosis can be expected, though perhaps more rarely, in *foetida* and thus provides for No. 33 the required genetic determination.

DISCUSSION

The incidence, at the Orrington site, of individuals with metameric and organ-locatica abnormality in the anterior part of the body (in front of 33/34) seems high. Percentages of similar abnormality, in collections from well-aerated and probably cooler beds of earthworm farms and also in the Darjiling series, are smaller; so much so as to indicate probability that unfavorable factors, in the Orrington habitat, were responsible for production of both sorts of aberrations. These abnormalities have been recorded from various other genera where a similar causation can be expected.

Homoeosis then originates, in *E. foetida* and in other lumbricids, in more than one way, at different times, and in one individual may be of single, double or even triple origin. Single-organ homoeosis, of the male terminalia (possibly also of the clitellum and of the tubercula pubertatis), is genetically determined before development. Homoeosis of more than one organ (or pair of organs) originates during embryogenesis or after hatching. Multi-organ homoeosis of embryonic origin may be one-sided or both-sided and then asymmetrical or symmetrical but even in cases of the latter sort may arise asymmetrically. Homoeosis of post-embryonic origin can be symmetrical if metamerism of the cephalic regenerate is normal and if there had been no asymmetry in the substrate that produced the new growth. After hypomeric regeneration, however, an original symmetrical homoeosis no longer may be recognizable.

Homoeosis may be either anterior or posterior when genetically determined or if resulting from regeneration, but always is posterior, except for minor subsequent regularizations, when induced during embryonic development. Cephalic regenerates with normal metamerism may be equimeric (and then not homoeotic in the Lumbricidae), hypo- or hyper-meric and producing, respectively, anterior or posterior homoeosis. Hypermery can be expected less frequently than hypomery. Hence, absence of anterior homoeosis, as in the Orrington series, provides justification for suspecting another origin than regeneration.

The homoeosis recorded in the literature was detected externally from location of reproductive apertures and of the clitellum. The latter organ varies, as to position and/or number of segments covered, in some species where it can evidence embryonically induced homoeosis only in more divergent and relictus-like individuals. The male pores most often have been cited as evidence of homoeosis but reference usually has been to conspicuous epidermal tumescences of the male terminalia for the real male pores are not only minute but also more or less deeply invaginate and rarely have been seen. Furthermore, male terminalia may be fully developed and homoeotic in adults of parthenogenetic strains that have no male pores. Also, the terminalia sometimes are doubled without increase in number of the male

pores. The female pores, unlike the male terminalia, appear not to be subject to mutational translocation from one segment to another and are reliable indicators, in the Lumbricidae, of embryonically induced homoeosis. However, even that evidence may be lacking because of inhibition of oviducal development or because of deflection of that duct so as to open externally through the ovarian segment rather than the one behind it. Hence, it seems possible that homoeosis occasionally will be undetectable externally.

The multi-organ homoeosis that has been considered above and in the preceding communications results from excalation or intercalation of segments. Homoeosis, however, means presence of organs in a segment other than that in which they normally belong. The first pair of testes, first pair of spermathecae, penultimate pair of hearts and the calciferous sacs, in certain species, all belong in x. Those same organs, after intercalations further forward could be in either the eleventh or the twelfth segment though still in exactly the same metamere where they would have been without the intercalations. There has been no translocation of organs nor assumption by one member of a series of characters belonging to another member of the same series, hence, strictly, multi-organ "homoeosis" is not actual but only apparent.

Intercalation of segments, except as a result of hypermeric regeneration, can arise only during embryonic development and then only by somite splitting. Whether the somites actually are, or are not, recognizable as discrete blocks makes no difference. The results are the same. Deletion of segments, except by post-hatching amputation, also must be of embryonic origin but is much rarer than intercalation and apparently results only from some sort of readjustment or regularization subsequent to somite splitting.

Intercalation of segments within the region from xv anteriorly is easily detectable because of the numerous organs that are not subject to mutational translocation. In the next region, from xvi to the hind end of the clitellum, intercalations can be detected externally only when the clitellum extends behind the posterior limit of individual variation. Internally, the gizzard, the only organ of fixed position in that region, sometimes does enable recognition of halving of somites at the sixteenth to the eighteenth levels. Lack of fixed-position organs behind the clitellum prevents recognition of segmental intercalations in that region, at least until after ascertainment of normal intraspecific variation as to segment number.

Doubling of fixed-position organs in aberrant lumbricids long ago was attributed to "doubling" of mesoblastic somites, but with specification only of those levels at which halving was most obvious. Attempts to locate all levels of splitting revealed, in several of the recently examined specimens, a small residuum of discordant homoeosis. Some of it is unexplained but the other portion seems to result from readjustments or regularizations subsequent to the intercalations.

The study of homoeotic earthworms has enabled, for animals not yet subjected to experimental modification of development, certain deductions as to morphogenesis. They are stated below in terms of lumbricid structure but when qualified according to anatomical differences should be valid also

for other families. Discovery of the environmental factors that operate to produce multi-organ homoeosis of embryonic origin should, however, provide better means of investigating earthworm morphogenesis.

SUMMARY

The homoeosis in a number of aberrant lumbricids having large differences as to degree of deviation from normal is explained, with maximum economy, by completely transverse subdivision of mesoblastic somites with retention by daughter somites (usually twins) of developmental potentialities of the parent block. A small residue of the homoeosis not so accounted for is attributed in part to subsequent regularizations which occasionally may involve some somite abortion.

Morphogenetic postulates deduced from the study of homoeosis are: Determination for differentiation of gonads and for development of male terminalia, clitellum, tubercula pubertatis, calciferous gland, terminal valve of the oesophagus, hearts and spermathecae, is a function of the original axial position of undivided mesoblastic somites. A testis induces development of seminal vesicles, a male funnel and deferent duct from its own septum and/or that next behind but only on its own side of the body. An ovary induces development of a female funnel and oviduct as well as of an ovisac but only on its own side of the body and only from the septum behind that bearing the gonad. Gonoduct development is anteroposteriorly polarized, the funnel rudiment proliferating toward the gonad, the duct rudiment away from it. Male gonoducts grow posteriorly until attracted into the parietes by the rudiments of the male terminalia. External segmentation, including development of setae at equatorial positions, is induced by or controlled from the mesoblast. Segmentation of the nerve cord is induced by the mesoblast and development of lateral nerves is controlled from the somites. The excretory system develops in accordance with the metamerism of the mesoblast. Development of a cocoon-secreting clitellum in the epidermis is induced, late in ontogeny, by mesodermal tissues. Invagination of the epidermis, also late in ontogeny, to produce spermathecae is induced from mesodermal tissues. Potentiality for development of male terminalia is subject to mutational transfer from one somite to another, anteriorly or posteriorly, with conservation, in both cases, of equatorial centering and meridional location.

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Racial Analysis of Clevelandia ios (Jordan and Gilbert) in Californian Waters[1]

Raghu R. Prasad

Within the total area of distribution of many species of fishes there exist what are called local races which can be distinguished by morphological and other characters. Investigations on the existence of such local races are important both in the field of systematics and that of fishery biology. In systematics racial differences blend into specific differences, while in fishery biology they are indicative of the segregation of populations and occupy an important place in the determination of separate fish stocks in relation to a given fishery.

Racial investigation is one of the aspects of fish population to which a great deal of attention has been devoted especially in Europe. One of the first workers who made a careful study of the differences between local populations of fishes was Heincke (1877). In his study of the herring (1898) he used both meristic characters and body proportions. Other investigators such as Matthews (1886 and 1887) on herring and Williamson (1900) on mackerel also used both morphometric and meristic characters. Other workers have limited their observations to fewer characters such as vertebral and fin-ray counts.

As to the causes of the morphological differences which characterize local populations, Hjort (1930) says that there is "somewhat sharp division of opinion between those who regard the formation of races as the result of fortuitous hereditary combinations of characteristics, and those who regard it as due to an interplay of the power of adaptation shown by the animals concerned and the physico-chemical conditions predominating in particular areas of the sea."

The belief that environmental conditions can and do alter the characters by which races are distinguished is based on the fact that such characters are not fixed but may vary from year to year in the same population. Schmidt (1930) is of the opinion that, although external factors are capable of altering the characters by which races of fishes are determined, it is quite wrong to ignore the fact that the differences in these characters by which races are determined may also be of an hereditary, genotypic nature. However, in all instances where racial investigations have been made on fishes, it has been shown that the physical and chemical conditions of the environment differ for each race. Tester (1938) remarks: "Considerable evidence has appeared in the literature in recent years to indicate that variation in the number of vertebrae and certain other meristic characters in fishes is caused in part at least by variation in environmental conditions, notably water temperature." At high temperatures the mean counts of vertebrae and fin-rays tend to be low, whereas the mean

[1] This investigation was carried out while the author was working at the Hopkins Marine Station, Pacific Grove, California. Present address: Central Marine Fisheries Research Station, Mandapam Camp, South India.

counts become progressively higher as the temperature becomes lower. The differences in the counts in other meristic characters found between different year-classes are also probably due entirely to environment. Tester (1938) from his observations on herrings concludes: "It follows that significant differences between the mean counts (of vertebrae) of year-classes in the same locality . . . are largely if not entirely due to annual differences in environmental conditions during the period between fertilization of the egg and ossification of the vertebral column. The results further indicate that the vertebra number of individual fish is already fixed within a short time after hatching." The same author (1937) showed also for *Clupea pallasii* that the mean vertebral count of a year-class increases with age and that the larger individuals of a year-class have a higher vertebral count. A note of caution has been sounded by Ford (1933) in the use of vertebral counts. He says: ". . . the nature and variation of the 'number of vertebrae' is such that particular caution is essential in interpreting the results of comparison between samples of herrings. We have to remember, not only that the 'number of vertebrae' is a statistical estimate of the corresponding character of the population sampled, and therefore subject to errors of sampling,' but also that the *population character* itself is one of considerable complexity."

Many investigators have pointed out that gobies show a high degree of variability. These variations may be ". . . différences suivant l'âge, différences sexuelles, différences apparaissant au moment de la maturité sexuelles, différences selon le milieu; aussi bien d'après le degré de concentration de l'eau, que d'après la nature du fond où vivent ces espèces" (Borcea, 1934).

While working on the life history of the gobiid fish, *Clevelandia ios,* it was thought that an investigation of the races in this species might yield some interesting results because these fish live both free and commensally in the tubes of the echiuroid worm *Urechis* and the burrows of the ghost shrimps *Callianassa* and *Upogebia* and do not migrate from one locality to another. The populations are thus restricted to definite areas and the chances of these mixing are rather few, although the transport of the pelagic larvae by coastwise currents must result in some admixture.

Acknowledgment.—I wish to express my sincere thanks to Drs. Rolf L. Bolin and Willis H. Rich for help and guidance, and to Mr. W. L. Follett for very kindly placing at my disposal the collections of *Clevelandia ios* in the California Academy of Sciences. Thanks are also due to my former colleagues at the Hopkins Marine Station for help rendered in the collection of material.

MATERIAL AND METHODS

The material for the study included specimens from four localities in California *viz.*, Elkhorn Slough, Mugu Lagoon, Mission Bay and Tijuana Slough (Fig. 1). The material from Elkhorn Slough was collected in December, 1946, that from Mugu Lagoon in October, 1945; the specimens from Mission Bay were taken on six different occasions between November, 1944, and April, 1946, while those from Tijuana Slough were captured in January, 1946. An attempt was made to collect specimens from near the northern limit of the range of the species; but without success. No *Clevelandia ios* were located in Oak Bay, Cadboro Bay or Saanichton Bay in Southern British Columbia.

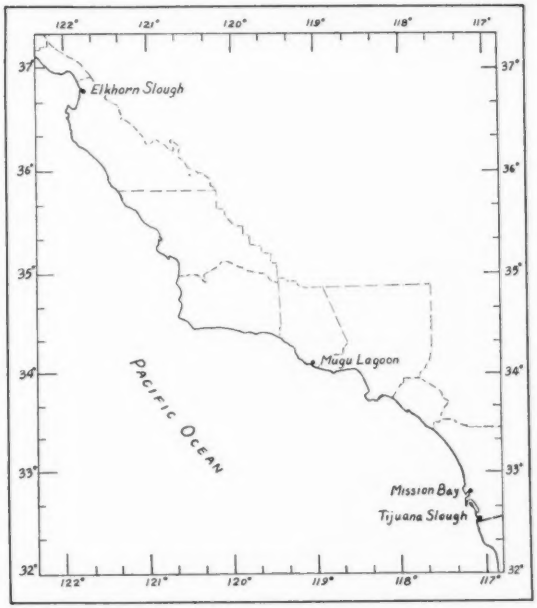

Fig. 1.—The coast of California showing the localities where *Clevelandia ios* were collected.

The problem has been approached by comparing both meristic and morphometric characters. Measurements of the length of head were made on specimens killed in 5 percent formaldehyde and preserved in 70 percent alcohol. The measurements, expressed to the nearest quarter of a millimeter by estimation, were made with the aid of needlepoint dividers by setting the dividers to the length to be determined and reading the span on a ruler marked into half-millimeter units. Fin-ray counts were made of all except the united ventral fins.[2]

Various statistical methods have been applied by different authors to test the significance of differences in the counts of vertebrae. Schnackenbeck (1931), who did extensive work on the herrings, employed the "shape" of the frequency polygon of vertebral number in a sample as the criterion of what he terms "mode of variability" of the sample. His methods have been criticised by Buchanan-Wollaston (1933) who recommends the use of Fisher's Analysis of Variance.

Our data on the meristic characters were first subjected to the *Analysis*

[2] In counting the rays of the caudal fin all branched and one unbranched fin-ray on either side of the branched rays have been included. Ginsburg (1945) remarks that a count of all the segmented rays, whether branched or unbranched, gives the best picture of this character.

of Variance to test all the samples for heterogeneity; the statistical significance of observed differences being determined by the *F*-ratio. Subsequently those characters which showed heterogeneity were further examined to ascertain the source of this heterogeneity. This was done by testing the significance of the difference (*d*) between pairs of means.[3]

As for the morphometric character, this was handled by the method of Analysis of Covariance. Morphometric measurements (e.g., length of head) are commonly treated as proportions of the total, or standard length. But this has disadvantages when, as is frequent, the proportion changes with size. In such cases the relation between the proportion and the total length is usually curvilinear and is difficult to describe and to interpret. A better method is to relate the length of the part, Y, (e.g., head) to the total or standard length, X. This relation is usually linear after the post-larval stages so that an *estimate* of the part, Y′, can be stated in terms of the length by the simple formula for a straight line, $Y' = a + bX$. The constant b measures the slope of the regression line and is known as the "regression coefficient." The regression line is easily described and interpreted and, in this form, morphometric characters are readily treated by the method of Analysis of Covariance. For details of Analysis of Variance and Analysis of Covariance see Kendall (1946). By this technique length of a part is "adjusted" for differences in total length and tests of heterogeneity are based on variances around regression lines rather than around means as in Analysis of Variances, but are similarly made by the use of appropriate *F*-ratios.

FIN-RAYS

The percentage distribution of the number of fin-rays of the first dorsal, second dorsal, anal, caudal and pectoral fins are shown in Figs. 2 to 6. The samples were tested for heterogeneity by the Analysis of Variance. The statistical details are given in Tables I, II, III, and IV.

It is seen from these tables that the samples show heterogeneity for only the first dorsal, second dorsal and anal fin-ray counts. The data for these three characters were again subjected to tests of significance to ascertain the source of heterogeneity. The statistics for these tests are given in Table IV.

In our interpretation of these statistics we have followed the common practice and accepted as significant all differences the probability of which, *P*, is less than .05. The evidence therefore indicates: 1) that the Elkhorn Slough population is different from the other three populations in all the meristic characters considered, 2) that the Mugu Lagoon fish differ significantly from those of Mission Bay and Tijuana Slough in the number of fin-rays of

[3] The formula used for calculating the standard error of the difference between means was:

$$\sigma_d = \sqrt{\frac{N_1}{N_2}\ \sigma\ M_1^{\,2} + \frac{N_2}{N_1}\ \sigma\ M_2^{\,2}}$$

the second dorsal and anal fins but not in the number of rays in the first dorsal fin, and 3) that the populations of Mission Bay and Tijuana Slough do not differ in any of these characters.

BODY MEASUREMENT

In addition to the meristic characters used in this study a single body measurement, the length of head, was also studied for heterogeneity. As mentioned earlier, the technique of *Analysis of Covariance* was employed to test whether the samples from different localities come from the same population or not. The associated characters chosen for the morphometric study were the length of head and standard length. The *Analyses of Covariance* are given in Tables V and VI.

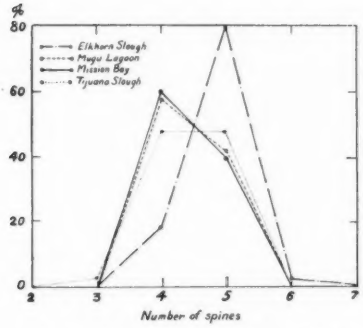

Fig. 2.—Percentage distribution of the spines of the first dorsal fin.

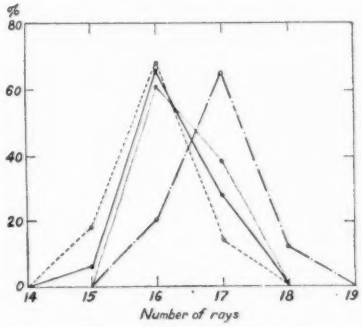

Fig. 3.—Percentage distribution of rays in the second dorsal fin.

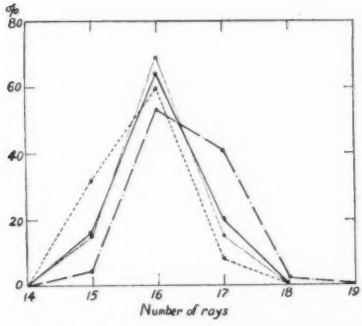

Fig. 4.—Percentage distribution of rays in the anal fin.

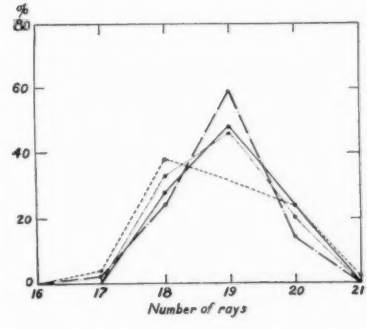

Fig. 5—Percentage distribution of rays in the pectoral fin.

TABLE I.—Data for analysis of variance, fin-ray counts.[4]

Fin		Locality				
		Elkhorn Slough	Mugu Lagoon	Mission Bay	Tijuana Slough	Total
	n	49	50	50	39	188
First Dorsal	SX	237	221	220	174	852
	mean	4.830	4.420	4.400	4.460	4.530
	SX^2	1155.000	989.000	980.000	788.000	3912.000
	$(SX)^2/n$	1146.306	976.820	968.000	776.307	3861.191
	Sx^2	8.694	12.180	12.000	11.693	50.809
	s^2	0.181	0.248	0.244	0.307	0.242
Second Dorsal	SX	829	798	811	639	3077
	mean	16.910	15.960	16.220	16.380	16.360
	SX^2	14041.000	12752.000	13169.000	10479.000	50441.000
	$(SX)^2/n$	14025.326	12736.080	13154.420	10469.769	50361.324
	Sx^2	15.674	15.920	14.580	9.231	79.676
	s^2	0.326	0.324	0.297	0.242	0.301
Anal	SX	804	788	802	624	3018
	mean	16.400	15.570	16.040	16.000	16.050
	SX^2	13210.000	12436.000	12882.000	9996.000	48524.000
	$(SX)^2/n$	13192.163	12418.880	12864.080	9984.000	48448.532
	Sx^2	17.837	17.120	17.920	12.000	75.468
	s^2	0.371	0.349	0.365	0.315	0.363
Pectoral	SX	924	941	948	736	3549
	mean	18.850	18.820	18.960	18.870	18.870
	SX^2	17446.000	17751.000	18000.000	13910.000	67107.000
	$(SX)^2/n$	17424.020	17709.620	17974.080	13889.641	66996.813
	Sx^2	21.980	41.380	25.920	20.359	110.187
	s^2	0.457	0.844	0.529	0.535	0.595
Caudal	SX	744	753	752	588	2837
	mean	15.180	15.060	15.040	15.070	15.090
	SX^2	11310.000	11347.000	11330.000	8878.000	42865.000
	$(SX)^2/n$	11296.653	11340.180	11310.080	8865.231	42811.537
	Sx^2	13.347	6.820	19.920	12.769	53.463
	s^2	0.278	0.139	0.406	0.336	0.286

[4] A common symbolism is employed in which X is the value of a single observation; x is the deviation of a single observation from the sample mean, s^2 is the variance (square of the standard deviation); n is the number of fishes in the sample; and S is the summation sign.

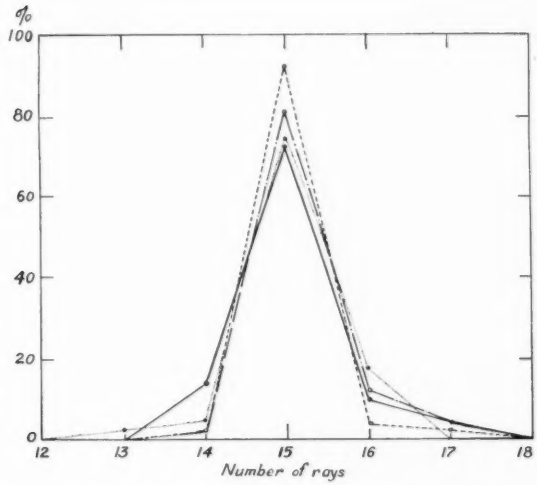

Fig. 6.—Percentage distribution of rays in the caudal fin.

TABLE II.—Analysis of variance, fin-ray counts.

Fin	Source of variation	Degrees of freedom	Sum of squares	Estimate of variance
First Dorsal	Individuals within localities	184	44.567	0.242
	Locality means	3	6.242	2.080
	Total	187	50.809	0.271
Second Dorsal	Individuals within localities	184	55.405	0.301
	Locality means	3	24.271	8.090
	Total	187	79.676	0.426
Anal	Individuals within localities	184	64.877	0.352
	Locality means	3	10.591	3.530
	Total	187	75.468	0.403
Pectoral	Individuals within localities	184	109.639	0.595
	Locality means	3	0.548	0.182
	Total	187	110.187	0.589
Caudal	Individuals within localities	184	52.856	0.287
	Locality means	3	0.607	0.202
	Total	187	53.463	0.285

TABLE III.—Test of significance.

Fin	F	P [5]
First Dorsal	8.59	<.001
Second Dorsal	26.87	<.001
Anal	9.72	<.001
Pectoral	0.30	>.5
Caudal	0.70	>.5

[5] Values of P (probability of chance occurrence) in this and other tables are from Fisher and Yates, 1948.

TABLE IV.—Statistics for the tests of significance of the differences between means of fin-rays ($t = d/\sigma_d$; P values from Fisher and Yates, Table III.).

Localities compared	First dorsal fin			
	σ_d	d	t	P
Elkhorn Slough, Mugu Lagoon	0.099	0.41	4.14	<.001
Elkhorn Slough, Mission Bay	0.099	0.43	4.34	<.001
Elkhorn Slough, Tijuana Slough	0.113	0.37	3.27	<0.1
Mugu Lagoon, Mission Bay	0.098	0.02	0.20	>.5
Mugu Lagoon, Tijuana Slough	0.112	0.04	0.35	>.5
Mission Bay, Tijuana Slough	0.112	0.06	0.53	>.5
	Second dorsal fin			
	σ_d	d	t	P
Elkhorn Slough, Mugu Lagoon	0.137	0.95	6.93	<.001
Elkhorn Slough, Mission Bay	0.135	0.69	5.11	<.001
Elkhorn Slough, Tijuana Slough	0.154	0.53	3.44	<.001
Mugu Lagoon, Mission Bay	0.111	0.26	2.34	<.02
Mugu Lagoon, Tijuana Slough	0.127	0.42	3.30	<.001
Mission Bay, Tijuana Slough	0.124	0.16	1.29	>.1
	Anal fin			
	σ_d	d	t	P
Elkhorn Slough, Mugu Lagoon	0.140	0.64	4.57	<.001
Elkhorn Slough, Mission Bay	0.141	0.36	2.55	<.02
Elkhorn Slough, Tijuana Slough	0.149	0.40	2.68	<.01
Mugu Lagoon, Mission Bay	0.118	0.28	2.37	<.02
Mugu Lagoon, Tijuana Slough	0.121	0.24	1.98	<.05
Mission Bay, Tijuana Slough	0.123	0.04	0.32	>.5

A comparison of the quotient 0.048 (178 d.f) with the quotient of the remaining items, 0.480 (6 d.f), obtained by pooling the sums of squares due to Differences b_j, Deviations of localities from b_m and Differences between b_a and b_m, and dividing this by the pooled degrees of freedom due to these items, indicates that there are real differences between localities, and that a single regression equation is not adequate to represent the relation between head length and body length in all localities (see also Fig. 7). It was further attempted to ascertain the source of heterogeneity in head length by testing the significance of the difference between the regression coefficients by using the formula for the standard error of the difference between the regression coefficients as given by Simpson and Roe (1939). The different values obtained by the above computations are given in Table VII (d_b is the difference and σd_b the standard error of the difference between regression coefficients).

TABLE V.—Analysis of covariance: Length of head.

Characters X	Characters Y	Source of Variation	n	d.f.	Sx^2	Sy^2	Sxy	b	r
Standard Length	Length of head	Elkhorn Slough	47	46	270.962	24.686	79.028	$b_1 = 0.291$	0.966
		Mugu Lagoon	50	49	290.290	23.126	75.965	$b_2 = 0.261$	0.927
		Mission Bay	50	49	251.787	16.488	60.394	$b_3 = 0.239$	0.937
		Tijuana Slough	39	38	90.656	5.314	17.950	$b_4 = 0.198$	0.817
		Within localities		182	903.695	69.614	233.337	$b_a = 0.258$	
		Between localities		3	32.470	7.510	14.471	$b_m = 0.445$	
		Total	186	185	936.165	77.124	247.808	$b_o = 0.264$	

TABLE VI.—Analysis of covariance: Length of head.[6]

Variation	d.f.	Sums S	Quotient
Deviations from regressions b_j	178	$S_1 = 8.646$	0.048
Differences b_j	3	$S_2 = 0.720$	0.240
Deviations from b_a	181	$S_1 + S_2 = 9.366$	0.051
Deviations of localities from b_m	2	$S_3 = 1.061$	0.530
Differences between b_a and b_m	1	$S_4 = 1.101$	1.101
Totals	184	$S_1 + S_2 + S_3 + S_4 = 11.528$	

[6] The notations used in this table are the same as those adopted by Kendall (1946) in his Table 24. 11.

The values of P show that the population from Elkhorn Slough differs significantly in the length of head from those of Mission Bay and Tijuana Slough but not from that of Mugu Lagoon. The significance of the difference in length of head between the samples of Mugu Lagoon and Tijuana Slough is approximately at the 3 percent level. The samples from Mugu Lagoon and Mission Bay as well as those from Mission Bay and Tijuana Slough do not show significant difference.

No attempt has been made to study other morphometric characters because the analyses have already shown that there are significant differences between populations with respect to the characters studied.

TABLE VII.—Test of significance of the difference between regression coefficients.

		Localities compared					
		Elkhorn Slough			Mugu Lagoon		Mission Bay
Characters		Mugu Lagoon	Mission Bay	Tijuana Slough	Mission Bay	Tijuana Slough	Tijuana Slough
Length of head	σd_b	0.019	0.017	0.024	0.020	0.029	0.025
	d_b	0.030	0.052	0.093	0.022	0.063	0.041
	$t = \frac{d_b}{\sigma d_b}$	1.57	3.05	3.87	1.10	2.17	1.64
	P	$> .1$	$< .01$	$< .001$	$> .2$	$< .05$	$> .1$

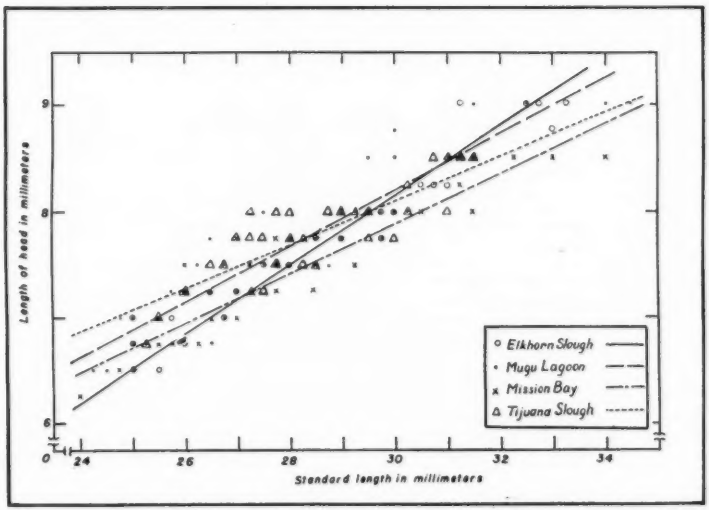

Fig. 7.—The regression of head length upon standard length for each region.

CONCLUSIONS

From the foregoing results the following general conclusions may be drawn. The population of Elkhorn Slough differs from that of Mugu Lagoon in three out of four characters selected for study and from those of Mission Bay and Tijuana Slough in all characters. The Mugu Lagoon population shows significant differences from that of Mission Bay in half the total number of the characters examined while it differs from the population of Tijuana Slough in three out of four characters. The populations of Mission Bay and Tijuana Slough show significant differences in none of the characters included in this study (Table VIII).

It is customary to distinguish and identify local populations by minor morphological characters and from a purely statistical standpoint the results indicate that there are three distinct populations viz., those of Elkhorn Slough, Mugu Lagoon and Mission Bay-Tijuana Slough. The results further suggest that the observed heterogeneity may be correlated with geographical origin as populations which are farther apart in their distribution show greater differences than those occurring more closely together. Thus, the population of Elkhorn Slough, the northernmost one examined, differs from the populations of the southernmost limit, Mission Bay and Tijuana Slough in all characters studied. The almost centrally located population (from Mugu Lagoon) differs in three, two and three characters respectively from the populations of Elkhorn Slough, Mission Bay and Tijuana Slough. However, it should be pointed out that duplicate samples were not collected from these localities for testing whether the samples within each locality is homogeneous from year to

TABLE VIII.—Differences in meristic and morphometric characters between the samples examined.

Localities compared	Characters			
	First dorsal fin-rays	Second dorsal fin-rays	Anal fin-rays	Length of head
Elkhorn Slough Mugu Lagoon	S	S	S	X
Elkhorn Slough Mission Bay	S	S	S	S
Elkhorn Slough Tijuana Slough	S	S	S	S
Mugu Lagoon Mission Bay	X	S	S	X
Mugu Lagoon Tijuana Slough	X	S	S	S
Mission Bay Tijuana Slough	X	X	X	X

S — Significantly different. X — not significantly different.

year. But it is unlikely that there is an intermingling of the different populations as this species is restricted in distribution to creeks and sloughs and are not known to undertake extensive migrations. They are usually found in shallow waters protected from heavy surf and in areas where there are large numbers of *Urechis*, *Callianassa* and *Upogebia* as the fish seek shelter in their burrows.

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Geographic Variation in Southeastern Populations of the Cyprinodont Fish Fundulus notti (Agassiz)

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Agassiz (1854) originally described the starhead topminnow under five specific names, *nottii, dispar, lineolatus, guttatus,* and *hieroglyphicus.* The present study demonstrates that this species consists of at least three well-defined subspecies, *notti, dispar,* and *lineolatus.* Each has prominent and parallel variation in coloration with sex and size. It is not surprising that Agassiz did not perceive the actual situation and was somewhat misled by the many color patterns displayed by these fishes. The nomenclatural confusion he generated still persists; consequently, for this species one of Agassiz's original five names must be chosen. Since Garman (1895) included them all in his synonymy under "*Fundulus nottii*", I recognize him as the first reviser and accordingly use *notti* as the species name. The names *guttatus* and *hieroglyphicus* are considered synonyms of *F. n. notti.*

This paper is primarily a study of the geographic variation in coastal plain populations of *Fundulus notti* from southern Virginia to Louisiana. For comparison a small sample of the subspecies found in the upper Mississippi River system (*dispar*) has also been included. Variation in the populations to the west and north of Louisiana has yet to be analyzed, but it is thought that significant variation does occur there. In particular the forms inhabiting Texas and Oklahoma should be studied, and the area where *F. n. notti* meets *F. n. dispar* should be determined as precisely as possible.

Acknowledgment.—I wish to thank Dr. Edward C. Raney, under whom the work was done as part of a review of the genus *Fundulus.* This was submitted as a Master's thesis at Cornell University in 1954. My thanks also go to Dr. Reeve M. Bailey for the loan of specimens of *F. notti dispar* from the University of Michigan Museum of Zoology.

Methods

Dorsal, anal, and pectoral rays were counted at their bases. The last two rays of the dorsal and anal fins were never counted as one, as has been the custom in counting for some species. Lateral line scales were counted according to the method of Hubbs and Lagler (1947) except that the most anterior scale counted was the one in which the center of the exposed field of the scale lay exactly on, or just posterior to, a vertical line through the upper extremity of the gill slit. For pectoral rays and lateral line scales, the counts of the left and right sides were added together; where only one side could be counted, the count was doubled. Scales around the caudal peduncle (usually, but not necessarily, the least count) were counted vertically at a point halfway between the posterior bases of the dorsal and anal fins and the anterior limits of the upper and lower procurrent caudal rays. Scales around the body were

counted in a complete ring encircling the body halfway between the anus and pelvic fin bases, and immediately anterior to the dorsal fin. When the scale immediately anterior to the dorsal origin was abnormal, the next normal scale row was used.

In the figures the range is shown as a single, heavy, horizontal line; the mean, by a short, pointed, vertical bar; one standard deviation on either side of the mean, by a hollow bar; and two standard errors on either side of the mean, by a solid black bar. Regardless of sample size the denominator used in calculating the standard deviation was always "N minus 1". In general, for normal distributions when the black bars for two samples do not overlap, it is safe to conclude that the difference between the two means is probably not due to chance. When the hollow bars do not overlap, an approximate separation of specimens of 84 percent or greater is indicated. Hubbs and Hubbs (1953) give details for interpreting this type of diagram. Because the distributions only approach normal, statistical interpretations should be made on the conservative side.

All descriptions of coloration were based on preserved specimens.

RESULTS

Fundulus notti consists of at least three distinct subspecies, the meristic and color characters of which are compared in Table VII. They may be characterized as follows:

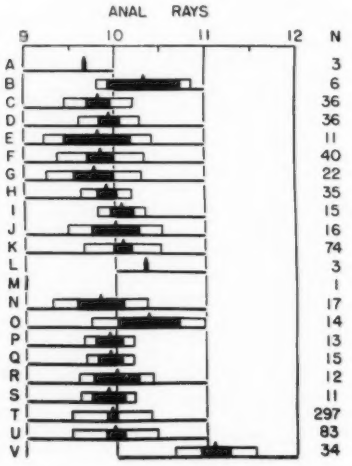

Fig. 1. — Number of anal rays in southeastern populations of *Fundulus notti*: *F. n. lineolatus* — A. Virginia and North Carolina; B. White Lake, North Carolina; C. Waccamaw River; D. Pee Dee River; E. South Carolina (Black, Edisto, Ashepoo, Combahee, and New Rivers); F. Ogeechee and Little Ogeechee Rivers; G. Altamaha River; H. Okefinokee Swamp (Suwannee River); I. St. Mary's River; J. Central Florida; K. Suwannee River, Florida and Georgia; L. Ochlockonee River. *F. n. notti* — M. New River, Florida; N. Apalachicola River; O. Choctawhatchee River; P. Yellow to Perdido Rivers; Q. Mobile Bay drainage; R. Pascagoula River; S. Pearl River to Lake Pontchartrain drainages. T. Total *F. n. lineolatus*; U. Total *F. n. notti*; V. Total *F. n. dispar*.

TABLE I.—Number of anal rays in southeastern populations of *Fundulus notti* (see also Fig. 1).

Populations	Number of Anal Rays							
	9	10	11	12	N	M	s	$2s_M$
lineolatus								
Va., N.C.	1	2	–	–	3	9.67	–	–
White Lake, N.C.	–	4	2	–	6	10.33	.52	.40
Waccamaw R.	6	30	–	–	36	9.83	.38	.13
Pee Dee R.	3	32	1	–	36	9.94	.33	.11
S.C.	3	7	1	–	11	9.82	.60	.36
Ogeechees R.	8	30	2	–	40	9.85	.48	.15
Altamaha R.	6	15	1	–	22	9.77	.53	.23
Okefinokee Swamp	3	32	–	–	35	9.91	.28	.10
St. Mary's R.	–	14	1	–	15	10.07	.26	.13
Central Fla.	2	12	2	–	16	10.00	.52	.26
Suwannee R.	4	60	10	–	74	10.08	.43	.10
Ochlockonee R.	–	2	1	–	3	10.33	–	–
notti								
New R., Fla.	1	–	–	–	1	9.00	–	–
Apalachicola R.	4	12	1	–	17	9.82	.53	.26
Choctawhatchee R.	1	7	6	–	14	10.36	.63	.34
Yellow to Perdido R.	1	12	–	–	13	9.92	.28	.15
Mobile Bay Drainage	1	14	–	–	15	9.93	.26	.13
Pascagoula R.	1	10	1	–	12	10.00	.41	.25
Pearl R. to Lake Pontchartrain	1	10	–	–	11	9.91	.30	.18
lineolatus	36	240	21	–	297	9.95	.44	.05
notti	10	65	8	–	83	9.98	.47	.10
dispar	–	2	27	5	34	11.09	.45	.16

Fundulus notti lineolatus (Agassiz)

All populations of *lineolatus* examined average close to 16 scales around the caudal peduncle, as contrasted with the usual 20 in the other two subspecies (Table V). This subspecies also averages lowest in scales around the body (Table IV and Fig. 4) but highest in lateral line scales (Table III and Fig. 3). The sides of the young of all three subspecies are marked with both the thick, dark, vertical bars of male adults and with the fine, dark, closely parallel, horizontal lines of female adults. In adults of *lineolatus* these markings are much more highly developed than in *notti*, the horizontal lines of females being dark, distinct, and clearly separate, and the vertical bars of males being especially dark and conspicuous.

Range.—Found from Nansemond County in southeastern Virginia south along the Atlantic coastal plain to central peninsular Florida and west along the Gulf coastal plain to the Ochlockonee River of Georgia and western Florida.

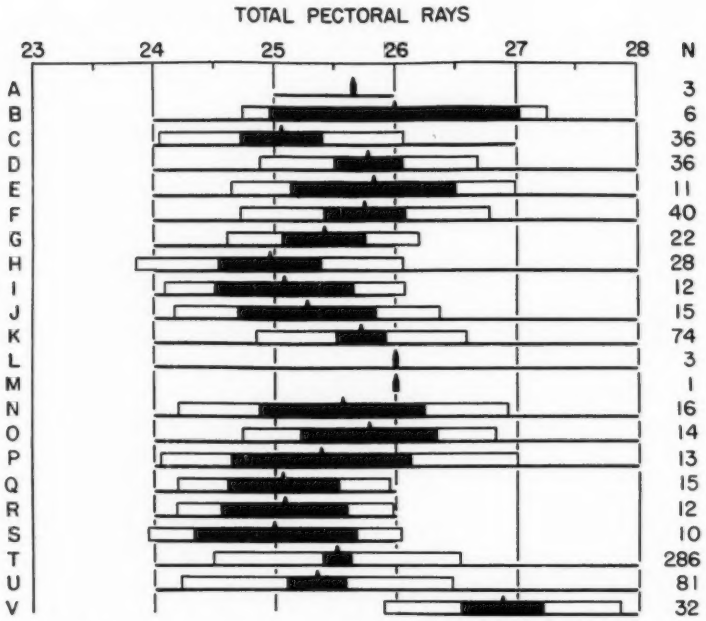

Fig. 2.—Total number of pectoral rays in southeastern populations of *Fundulus notti:* A.-V. Same as Fig. 1.

Material examined.—VIRGINIA. NANSEMOND CO.: Trib. Nansemond R. 2 mi. N. of Suffolk (CU 9918, 1 specimen). NORTH CAROLINA. DUPLIN CO.: Middleton Mill Creek 2.5 mi. W. of Kenansville (CU 9753, 1). GATES CO.: Sunbury, Rt. 32, Chowan system (CU 9883, 1). BLADEN CO.: White Lake (CU 15648, 6). COLUMBUS CO.: Canal off Waccamaw R. 1 mi. N. of Waccamaw R., Rt. 130, near Ashe (CU 14289, 36). MOORE CO.: Aberdeen Lake, Aberdeen (CU 11125, 18); Aberdeen Creek below dam, Aberdeen, Rt. 1 (CU 19772, 1). RICHMOND CO.: Mark Creek, Evers Mill (CU 14285, 2). SOUTH CAROLINA. FLORENCE CO.: Middle Swamp 3 mi. S. of Florence, Rt. 52 (CU 19184, 3); Trib. Lynches R. 1 mi. W. of Timmonsville (CU uncataloged, 1). DILLON CO.: Buck Sap, trib. Little Pee Dee R. 5.5 mi. SW. of Dillon (CU 15861, 1). CHESTERFIELD CO.: Trib. Pee Dee R. 2 mi. NW. of Society Hill (CU 15634, 4). DARLINGTON CO.: Trib. Pee Dee R. Society Hill (CU 15715, 5). MARLBORO CO.: White's Creek, trib. Pee Dee R. 5.5 mi. N. of Cherow, Rt. 1 (CU 15482, 1). SUMTER CO.: Trib. Pocotaligo R. 1 mi. W. of Sumter (CU 15379, 2). ORANGEBURG CO.: Trib. North Fork of Edisto R. (CU 15401, 1). COLLETON CO.: Ireland Creek, trib. Ashepoo R. (CU 12280, 2). BAMBERG CO.: Little Salkehatchie R. between Denmark and Hilda, Rt. 70 (CU 19197, 5). JASPER CO.: Great Swamp, trib. New R. (CU 15413, 2). GEORGIA. BRYAN CO.: 5 mi. NW. Richmond Hill (CU 15579, 7); Trib. Black Creek 5.8 mi. S. of Blichton (CU 15452, 4). BULLOCH CO.: Lotts Creek 7.4 mi. S. of Statesboro, Rt. 25 (CU 17474, 11). CANDLER CO.: Canoochee R. 4.9 mi. W. of Melter, Rt. 46 (CU 17227, 8). CHATHAM CO.: Trib. Little Ogeechee R. 5.4 mi. W. of Bloomingdale (CU 15420, 6). BRYAN AND EVANS CO. line: Canoochee R. 2.3 mi. W. of Groveland, Rt. 280 (CU 15117, 4). EMANUEL CO.: Little Ohoopee R. 9.2 mi. W. of Swainsboro, Rt. 80 (CU 17191, 3); trib. Ohoopee R. 15.2 mi. W. of Swainsboro, Rt. 80, CU 17692, 5). WILCOX CO.: Oswitchee Springs 2 mi. E. of Forest Glen (CU 17614, 2). DODGE

TABLE II.—Total number of pectoral rays in southeastern populations of *Fundulus notti* (see also Fig. 2).

Populations	Total Pectoral Rays					N	M	s	$2s_M$
	24	25	26	27	28				
lineolatus									
Va., N.C.	–	1	2	–	–	3	25.67	–	–
White Lake, N.C.	1	0	4	0	1	6	26.00	1.27	1.03
Waccamaw R.	16	3	16	1	–	36	25.06	1.01	.34
Pee Dee R.	4	5	24	1	2	36	25.78	.90	.28
S.C.	2	1	6	1	1	11	25.82	1.17	.68
Ogeechees R.	7	4	23	4	2	40	25.75	1.03	.33
Altamaha R.	4	5	13	–	–	22	25.41	.80	.34
Okefinokee Swamp	14	3	10	0	1	28	24.96	1.11	.42
St. Mary's R.	5	1	6	–	–	12	25.08	1.00	.58
Central Fla.	5	4	4	1	1	15	25.27	1.10	.57
Suwannee R.	12	4	52	5	1	74	25.72	.87	.20
Ochlockonee R.	1	0	1	0	1	3	26.00	–	–
notti									
New R., Fla.	–	–	1	–	–	1	26.00	–	–
Apalachicola R.	5	2	6	1	2	16	25.56	1.37	.68
Choctawhatchee R.	2	2	8	1	1	14	25.78	1.05	.56
Yellow to Perdido R.	5	1	5	1	1	13	25.38	1.33	.74
Mobile Bay Drainage	5	4	6	–	–	15	25.07	.88	.46
Pascagoula R.	4	3	5	–	–	12	25.08	.90	.52
Pearl R. to Lake Pontchartrain	5	0	5	–	–	10	25.00	1.05	.67
lineolatus	71	31	161	13	10	286	25.51	1.02	.12
notti	26	12	36	3	4	81	25.34	1.12	.25
dispar	–	–	17	2	13	32	26.88	.98	.35

CO.: Trib. Ocmulgee R. just E. of Rhine, Rt. 280 (CU 17705, 4). TELFAIR CO.: Little Ocmulgee R. 1.2 mi. N. of McRae, Rt. 319 (CU 17255, 5). WAYNE CO.: Trib. Penholoway R. 2 mi. NE. of Jessup (CU 12817, 3). CHARLTON CO.: Billy's I. (CU 41, 43-49, 8; CU 111-115, 5; CU 243-245, 3; CU 319, 1; CU 242, 1; CU 140-142, 3; CU 531, 2; CU 33-40, 8; CU 8714, 1); prairies S. of Honey I. (CU 8710, 1); Floyd's I. Prairie (CU 8715, 3); trib. St. Mary's R. 1.7 mi. SW. of Folkston, Rt. 23 (CU 21078, 2); Thompson Landing, Folkston (CU 518, 1); Starling Branch Crossing, Folkston (CU 514, 2); Clay Branch, Folkston (CU 4041, 5). BERRIEN CO.: Trib. Alapaha R. 4.7 mi. E. of Nashville, Big Creek (CU 15729, 19). WILCOX CO.: Trib. Alapaha R. 0.6 mi. W. of Pitts, Rt. 280 (CU 17404, 1). COLQUITT CO.: Trib. 1.2 mi. W. of Funston, Rt. 37 (CU 17503, 1). LANIER CO.: Five Mile Creek, trib. Alapaha R., eastern limits Lakeland (CU 15435, 31). FLORIDA. NASSAU CO.: Trib. Nassau R. 12 mi. W. of Yulee, Rt. 200 (CU 12420, 1); jct. Rt. 119, Rt. 200, 6 mi. S. of Bryceville (CU 12414, 1). BAKER CO.: South Prong St. Mary's R. 1.4 mi. W. of Macclenny, Rt. 90 (CU 12614, 3). LEVY CO.: Waccasassa R. 5 mi. NW. of Bronson (CU 12792, 1); 2.8 mi. N. of Gulf Hammock, Waccasassa R. (CU 12814, 8). OSCEOLA CO.: 4 mi. SW. of St. Cloud (CU 10235, 4). VOLUSIA CO.: 10 mi. W. of Daytona (CU 4086, 1). COLUMBIA CO.: 2 mi. S. of Benton (CU 12505, 16). ALACHUA CO.: Waldo (CU 2525, 3); Lake Jackson (CU 2532, 4). LEON CO.: Trib. Ochlockonee R. 19 mi. W. of Tallahassee (CU 12367, 2).

TABLE III.—Total number of lateral line scales in southeastern populations of *Fundulus notti* (see also Fig. 3).

Populations	Total Lateral Line Scales								
	60	61	62	63	64	65	66	67	68
lineolatus									
Va., N. C.	–	–	–	1	1	1	–	–	–
White Lake, N.C.	–	–	–	–	–	–	–	1	2
Waccamaw	–	–	–	–	3	5	8	8	9
Pee Dee R.	–	–	1	0	3	3	15	6	7
S. C.	–	–	–	–	–	2	4	3	1
Ogeechees R.	–	–	–	–	–	3	6	7	15
Altamaha R.	–	–	–	–	3	2	5	4	5
Okefinokee Swamp	–	–	–	–	2	4	8	2	6
St. Mary's R.	–	–	–	–	–	1	5	2	2
Central Fla.	–	–	–	–	1	0	1	3	6
Suwannee R.	–	–	–	1	2	5	15	13	27
Ochlockonee R.	–	–	–	–	–	–	–	–	1
notti									
New R., Fla.	–	–	–	–	–	–	–	1	–
Apalachicola R.	–	–	–	–	–	5	6	5	0
Choctawhatchee R.	–	–	–	1	2	1	6	1	3
Yellow to Perdido R.	–	–	–	–	1	5	3	2	2
Mobile Bay Drainage	–	–	–	–	2	0	4	5	4
Pascagoula R.	–	–	–	–	1	4	3	4	5
Pearl R. to Lake Pontchartrain	–	–	–	–	1	4	3	2	–
lineolatus	–	–	1	2	15	26	67	49	81
notti	–	–	–	1	7	19	25	20	9
dispar	1	2	0	9	7	7	7	1	–

TABLE III.—(*continued*).

Populations	Total Lateral Line Scales				N	M	s	$2s_M$
	69	70	71	72				
lineolatus								
Va., N. C.	–	–	–	–	3	64.00	–	–
White Lake, N.C.	1	–	–	–	4	68.00	.82	.82
Waccamaw R.	3	–	–	–	36	66.66	1.43	.48
Pee Dee R.	–	–	–	–	35	66.20	1.24	.42
S. C.	0	1	–	–	11	66.64	1.43	.86
Ogeechees R.	5	3	–	–	39	67.56	1.33	.43
Altamaha R.	1	1	–	–	21	66.62	1.66	.72
Okefinokee Swamp	3	1	–	–	26	66.73	1.64	.64
St. Mary's R.	1	1	–	–	12	67.00	1.48	.85
Central Fla.	3	1	–	–	15	67.73	1.44	.74
Suwannee R.	5	4	0	1	73	67.26	1.55	.36
Ochlockonee R.	1	1	–	–	3	69.00	–	–
notti								
New R., Fla.	–	–	–	–	1	67.00	–	–
Apalachicola R.	1	–	–	–	17	66.18	1.08	.52
Choctawhatchee R.	–	–	–	–	14	65.93	1.54	.82
Yellow to Perdido R.	–	–	–	–	13	65.92	1.26	.70
Mobile Bay Drainage	–	–	–	–	15	66.60	1.30	.67
Pascagoula R.	5	–	–	–	12	65.83	1.05	.59
Pearl R. to Lake Pontchartrain	–	–	–	–	10	65.60	.97	.61
lineolatus	23	13	0	1	278	66.98	1.57	.19
notti	1	–	–	–	82	66.06	1.22	.27
dispar	–	–	–	–	34	64.15	1.62	.55

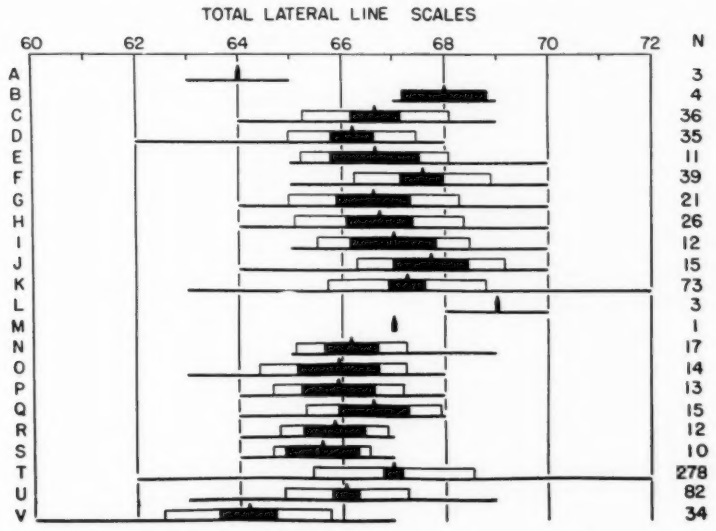

Fig. 3.—Total number of lateral line scales in southeastern populations of *Fundulus notti*: A.-V. Same as Fig. 1.

Range.—Found from the New River of western Florida west along the Gulf coastal plain to Louisiana and eastern Texas (subspecies uncertain, Knapp, 1954).

FUNDULUS NOTTI NOTTI (Agassiz)

This subspecies cannot be characterized by any single meristic character known to the author. In lateral line scales and scales around the body it averages between *dispar* and *lineolatus*. In number of anal rays it is similar to *lineolatus;* and in scales around the caudal peduncle it is similar to *dispar*. In coloration, however, it is unique. Adult females lack the distinct horizontal lines of *lineolatus* and *dispar*. Lines are actually present but they are indistinct and are connected by vertical lines of equal width and intensity which effect the impression of parallel rows of light spots. In a few large females the pigment causing the above effect is faded and a dark spot on each body scale is evident. In males these dark pigment spots are often irregularly arranged; consequently, great individual variation exists in color pattern. The tendency toward disruption of straight lines and lightening of pigment is strong in *notti* as compared with the clean-appearing *lineolatus* and *dispar*.

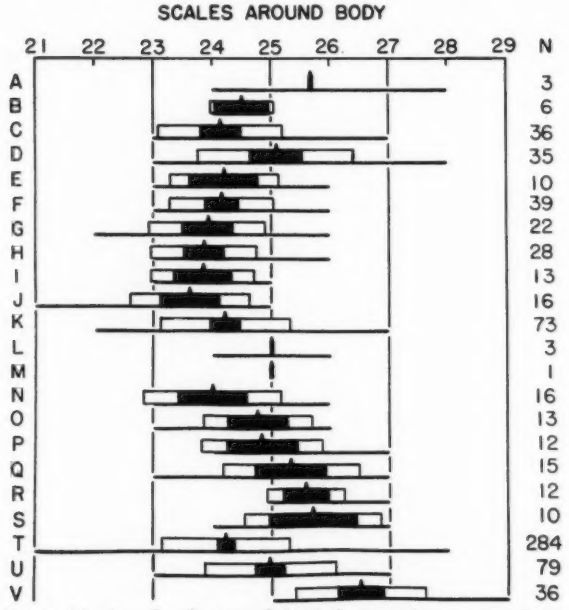

Fig. 4. Number of scales around the body in southeastern populations of *Fundulus notti:* A-V. Same as fig. 1.

TABLE IV.—Number of scales around the body in southeastern populations of *Fundulus notti*. (See also Fig. 4.)

Populations	Scales around Body						
	21	22	23	24	25	26	27
lineolatus							
Va., N. C.	–	–	–	1	1	0	0
White Lake, N.C.	–	–	–	3	3	–	–
Waccamaw R.	–	–	11	14	7	3	1
Pee Dee R.	–	–	5	8	6	12	3
S. C.	–	–	2	5	2	1	–
Ogeechees R.	–	–	11	12	15	1	–
Altamaha R.	–	1	7	8	5	1	–
Okefinokee Swamp	–	–	11	12	3	2	–
St. Mary's R.	–	–	6	3	4	–	–
Central Fla.	1	1	3	9	2	–	–
Suwannee R.	–	2	15	35	11	7	3
Ochlockonee R.	–	–	–	1	1	1	–
notti							
New R., Fla.	–	–	–	–	1	–	–
Apalachicola R.	–	–	4	9	2	1	–
Choctawhatchee R.	–	–	2	1	8	2	–
Yellow to Perdido R.	–	–	–	6	3	2	1
Mobile Bay Drainage	–	–	1	2	6	3	3
Pascagoula R.	–	–	–	–	6	5	1
Pearl R. to Lake Pontchartrain	–	–	–	2	2	3	3
lineolatus	1	4	71	111	60	28	7
notti	–	–	7	20	28	16	8
dispar	–	–	–	–	7	12	11

TABLE IV.—(*continued.*)

Populations	Scales around Body					
	28	29	N	M	s	$2s_M$
lineolatus						
Va., N. C.	1	–	3	25.67	–	–
White Lake, N.C.	–	–	6	24.50	.55	.45
Waccamaw R.	–	–	36	24.14	1.05	.35
Pee Dee R.	1	–	35	25.09	1.34	.45
S. C.	–	–	10	24.20	.92	.58
Ogeechees R.	–	–	39	24.15	.87	.28
Altamaha R.	–	–	22	23.91	.97	.41
Okefinokee Swamp	–	–	28	23.86	.89	.34
St. Mary's R.	–	–	13	23.85	.90	.50
Central Fla.	–	–	16	23.62	1.03	.51
Suwannee R.	–	–	73	24.21	1.09	.26
Ochlockonee R.	–	–	3	25.00	–	–
notti						
New R., Fla.	–	–	1	25.00	–	–
Apalachicola R.	–	–	16	24.00	1.16	.58
Choctawhatchee R.	–	–	13	24.77	.93	.51
Yellow to Perdido R.	–	–	12	24.83	1.03	.59
Mobile Bay Drainage	–	–	15	25.33	1.18	.61
Pascagoula R.	–	–	12	25.58	.67	.39
Pearl R. to Lake Pontchartrain	–	–	10	25.70	1.16	.73
lineolatus	2	–	284	24.22	1.11	.13
notti	–	–	79	24.97	1.11	.25
dispar	4	2	36	26.50	1.11	.37

Material examined.—FLORIDA. LIBERTY CO.: 2 mi. S. of Vilas (CU 12381, 1 specimen); Trib. Owl Creek, Rowlett's Creek, Wilma Ranger Sta. (CU 12452, 3). CALHOUN CO.: Trib. Chipola R. 3.3 mi. W. of Blountstown, Rt. 20 (CU 12089, 4); Sugar Creek, trib. Chipola R. 6.9 mi. W. of Clarksville (CU 12682, 2); trib. Chipola R. 38 mi. W. of Blountstown, Rt. 20 (CU 18166, 2). JACKSON CO.: Trib. Chipola R. 3.4 mi. NW. of Cottondale, Rt. 169 (CU 17182, 2). HOLMES CO.: 7.2 mi. E. of De Funiak Springs (CU 22053, 12); Reedy Creek 4 mi. SW. of Westville (CU 12696, 1); Sandy Creek, Ponce de Leon (CU 12114, 1). WALTON CO.: Gum Creek, trib. Shoal R. 5.9 mi. NW. of De Funiak Springs (CU 12118, 3). ALABAMA. HOUSTON CO.: Chipola R. 0.9 mi. NW. of Grangeburg (CU 17677, 2). ESCAMBIA CO.: Trib. Conecuh R. 9.4 mi. W. of Dixie, Rt. 29 (CU 14053, 3); Brushy Creek, trib. Perdido R. 2.8 mi. W. of Atmore, Rt. 31 (CU 12631, 3); Brushy Creek, trib. Perdido R. 2.9 mi. SW. of Atmore (CU 14051, 4). BALDWIN CO.: Trib. Fish R. 10.2 mi. W. of Robertsdale, Rt. 90 (CU 16666, 3). WASHINGTON CO.: Trib. Basset Creek; Gaines Creek 2.8 mi. S. of Leroy (CU 16164, 2); 1.8 mi. W. of Wagerville, Rt. 84, (CU 16173, 9). MOBILE CO.: Trib. Chickasaw Creek 5.2 mi. E. of Semmes, Rt. 42 (CU 12635, 1); Big Creek 5.3 mi. W. of Semmes, Rt. 42 (CU 12458, 6). GEORGIA. DOUGHERTY CO.: Kiokee Creek, trib. Chickasawhatchee Creek 3.2 mi. W. of Pretoria, Rt. 62 (CU 17684, 2). MISSISSIPPI. LAMAR CO.: Trib. Black (?) Creek 6.9 mi. W. of Forrest Co. line (CU 15629, 2). WAYNE CO.: Trib. Chickasawhay Creek 7.2 mi. NW. of Bucatunna (CU 16243, 4). PEARL RIVER CO.: Trib. Wolf R. 8.6 mi. E. of Poplarville (CU 16628, 2). LOUISIANA. TANGIPAHOA PARISH: Trib. Selser Creek, 3.3 mi. E. of Hammond, Rt. 190 (CU 13940, 5); 4.2 mi. W. of Robert, Rt. 190 (CU 21534, 4).

TABLE V.—Number of scales around the caudal peduncle in southeastern populations of *Fundulus notti*. (Because of their skewed distribution these data have not been treated statistically.)

Populations	Scales around Caudal Peduncle						
	16	17	18	19	20	N	M
lineolatus							
White Lake, N.C.	1	3	1	1	–	6	17.3
Waccamaw R.	27	0	3	–	–	30	16.2
Okefinokee Swamp	30	1	1	–	–	32	16.1
St. Mary's R.	7	–	–	–	–	7	16.0
St. John's R.	2	–	–	–	–	2	16.0
Suwannee R.	46	2	6	1	–	55	16.3
Ochlockonee R.	3	–	–	–	–	3	16.0
notti							
New R., Fla.,	–	–	–	–	1	1	20.0
Apalachicola R.	–	–	4	4	9	17	19.3
Choctawhatchee R.	–	–	1	3	10	14	19.6
Yellow R.	–	–	–	1	2	3	19.7
Escambia R.	–	–	–	–	3	3	20.0
Perdido R.	–	–	1	0	6	7	19.7
Mobile Bay Drainage	–	–	1	3	11	15	19.7
Escatawpa R.	–	–	1	1	4	6	19.5
Pascagoula R.	–	–	–	–	6	6	20.0
Pearl R.	–	–	–	–	2	2	20.0
Pontchartrain Drainage	–	–	–	2	5	7	19.7
lineolatus	116	6	11	2	–	135	16.3
notti	–	–	8	14	59	81	19.6
dispar	–	–	–	2	32	34	19.9

TABLE VI.—Number of dorsal days in the subspecies of *Fundulus notti*.

Subspecies	Number of Dorsal Rays					
	6	7	8	9	N	M
lineolatus	1	20	244	28	293	8.02
notti	–	8	70	4	82	7.95
dispar	–	2	26	2	30	8.00

FUNDULUS NOTTI DISPAR (Agassiz)

Anal rays in *dispar* average 11 rather than 10 as in *notti* and *lineolatus* (Table I, Fig. 1); pectoral rays also average higher in *dispar* (Table II, Fig. 2). Lateral line scale counts average lowest in *dispar* of the three subspecies Table III, Fig. 3) while the number of scales around the body averages highest (Table IV, Fig. 4). In coloration *dispar* is close to *lineolatus*, being distinguishable only by subtleties which may not prove to be consistent. In general it seems neither as heavily nor as evenly patterned.

Range.—Found in the Mississippi Valley from Iowa, southern Wisconsin, and the Lake Michigan drainage of Michigan and Indiana south to northeastern Arkansas and western Tennessee (Hubbs and Lagler, 1947).

TABLE VII.—Comparisons of the subspecies of *Fundulus notti*.

Character	*lineolatus*	*dispar*	*notti*
Scales around caudal peduncle	16-17 (16-19)	18-20	18-20
Anal rays	Usually 10	Usually 11	Usually 10
Total pectoral rays	Average 25.5 (24-28)	Average 27 (26-28)	Average 25 (24-28)
Total lateral line scales	Average 67.0 (62-72)	Average 64.3 (60-67)	Average 65.9 (60-69)
Scales around body in front of dorsal fin and anus	Average 24.4 (21-28)	Average 26.5 (25-29)	Average 25.1 (23-29)
Dark longitudinal lines between scale rows on sides of body; a single line being composed of dark edges of scales above and below it	Females: Heavy, dark, unbroken	Females: Narrow, dark, unbroken	Females: Indistinct, not dark, fade to virtual absence in large adults
	Males: Pale to absent	Males: Pale to absent, stronger posteriorly	Males: Pale to absent, stronger posteriorly
Posterior edges of scales on sides of body	Females: With no border of melanophores	Females: With border of melanophores absent or faint	Females: with border of melanophores as dark and wide as longitudinal lines running between scale rows. Males: Border of melanophores as dark or darker than longitudinal lines, especially on upper sides
	Males: Border faint or absent	Males: Border faint or absent	
Dark dots in centers of scales on sides of body	Females: Absent in adult Males: Generally small, in regular rows, of even intensity for length of body	Females: Usually absent Males: Generally small, in regular rows, particularly distinct anteriorly	Females: Regularly arranged in rows; strikingly prominent in large adults. Males: Often large, in rows or irregularly arranged, of variable intensity
Cross bars of males	Strong, dark, uniform intensity from head to tail, wide	Dark, fainter anteriorly, narrow	Lighter, fainter anteriorly, narrow
Range	Ochlockonee R. of W. Fla., east and north in Atlantic Coast river systems to SE. Va.	Mississippi Valley: Iowa, S. Wisc., and Lake Michigan drainage of Mich. and Ind. southward to NE. Ark. and W. Tenn.	Gulf Coast river systems from New River of W. Fla. westward to Texas

Material Examined.—INDIANA. GREENE CO.: Switz City (CU 1858, 2 specimens). CLARK CO.: (CU 2969, 4). MICHIGAN. BRANCH CO.: Crooked or Dragon Lake (UMMZ 90149, 5); Bawbesse Lake (UMMZ 60564, 5). HILLSDALE CO.: Fifth Lake (UMMZ 98010, 4). ILLINOIS. UNION CO.: Azalea Bluff Spring, La Rue or Aldridge (UMMZ 105834, 7); Wolf Lake (UMMZ 162874, 2). TENNESSEE. HAYWOOD CO.: Muddy Creek 3 mi. NE. of Stanton (UMMZ 161023, 8).

DISCUSSION

Frey (1951) noticed that specimens from White Lake, North Carolina, differ slightly in a number of characters from typical *lineolatus*. These differences are apparently associated with the almost complete absence of dissolved color in White Lake and the high pH, both of which are correlated with a number of other environmental factors which may have a strong selective effect on fish populations. The small sample from White Lake included in the present study shows a high number of scales around the caudal peduncle. Frey also reported a higher number of lateral line scales than his average for other *lineolatus*, but the present data give meager support for this. In coloration the general aspect of White Lake specimens suggests that of *F. n. dispar*, being not as boldly and heavily marked as typical *lineolatus*.

All specimens examined from the range of *notti* are definitely assignable to that subspecies; no specimens of *notti* were found in the range of *lineolatus*. The one specimen from the New River of western Florida is definitely *notti*, both by coloration and scale counts; the three specimens from the Ochlockonee River are definitely *lineolatus*. Thus the two forms have not been shown to exist sympatrically, nor have they been shown to intergrade.

The status of *lineolatus* and *notti* in Crooked River, a coastal stream which connects the New and Ochlockonee Rivers and which may present possibilities for gene flow between the two populations, remains unknown. The area where *notti* meets *dispar* is even less well-defined. When it is known, the extent to which *notti* interbreeds naturally with *lineolatus* and *dispar* will determine whether they rate the distinction of full species. In order to avoid a nomenclatural change without the support of proper evidence they have been retained in this paper in their customary status as subspecies.

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Morphology of Two Chalcidoid Parasites of Ticks, Hunterellus hookeri Howard, 1908, and Ixodiphagus texanus Howard, 1907*

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Howard in 1907 described the first insect parasite of ticks from nymphs of *Haemaphysalis leporis-palustris*. He erected a new genus *Ixodiphagus* for this parasite and described this new species as *I. texanus*. He placed the genus in the family Encyrtidae Walker, 1837, and in the subfamily Encyrtinae Howard, 1886.

In 1908 the above author described another chalcidoid parasite of ticks from the dog tick, *Rhipicephalus sanguineus* (Latreille). A new genus *Hunterellus* was erected by Howard for this species, *H. hookeri*. In the same paper Howard also proposed a new tribe, Ixodiphagini, to include both of his genera, *Ixodiphagus* and *Hunterellus*.

Du Buysson in 1912 described another chalcidoid parasite *Ixodiphagus caucurtei* from France.

Gahan in 1934 pointed out that "a paper by R. A. Cooley published in 1929 apparently implies (p. 267) that all three of these names refer to the same insect." Gahan, however, shows that *Ixodiphagus texanus* and *Hunterellus hookeri* are quite distinct species, while *I. caucurtei* is identical with *H. hookeri*. In the same paper Gahan has also given a dichotomy for the separation of the two species and a very short description of each.

Smith and Cole (1943) follow Gahan in regarding *I. texanus* and *H. hookeri* as distinct species, and *I. caucurtei* du Buysson a synonym of *H. hookeri*.

To date, therefore, only two insect parasites of ticks are recognized and the present work is a study of their morphology. In the following pages, the morphology of *H. hookeri* is described in detail; while in the case of *I. texanus*, points of difference from *H. hookeri* have been mentioned.

Figures to show many of the external anatomical features have been drawn for *H. hookeri;* and in the case of those parts in which the differences

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* Portion of a thesis submitted to the University of Massachusetts in partial fulfillment of the degree of Doctor of Philosophy.

between the two species are pronounced, figures have also been drawn for *I. texanus* for comparison.

HUNTERELLUS HOOKERI Howard, 1908

GENERAL EXTERNAL MORPHOLOGY

It is a small insect, blackish in color, with typical chalcidoid appearance. Specimens (♂ and ♀) preserved in alcohol are 0.8-0.9 mm in length and have a wing expanse of 1.5 mm.

The specimens for study were boiled in a 2 to 3 percent aqueous solution of caustic potash (KOH) and the following measurements (in millimeters) were recorded.

	Length	Width
Male		
Entire body	1.2-1.4	1.5-1.6 (wing expanse)
Head	0.24	0.42
Thorax	0.58	0.42
Abdomen	0.54	0.48
Female		
Entire body	1.2-1.4	1.5-1.6 (wing expanse)
Head	0.24	0.44
Thorax	0.6	0.48
Abdomen	0.62	0.54

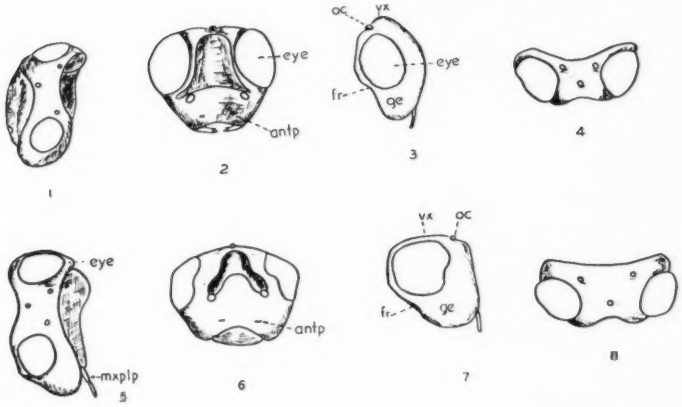
The measurements in length were made along the mid-line, while those in width were made at the widest place.

HEAD

The head of *Hunterellus hookeri* is somewhat flattened dorsally (Figs. 5-8). The frontal region of the head (Fig. 7) makes a sharp angle with the vertical, and thus directs the mouthparts posteroventrally making the head slightly opisthognathous. The head is twice as wide as it is long. The compound eyes are very prominent at the sides and the width of the head is greatest at the compound eyes. The antennae are located in front and are close to each other. The three ocelli are located dorsally.

Sutures of the head capsule.—All sutures of the head capsule, except the antennal and ocular, have been lost in this species. The various areas of the head can, however, be demarcated by other landmarks.

Areas of the head capsule.—The vertex (Fig. 7, vx) is formed by the top of the head. The frons is limited posteriorly by the median ocellus, anteriorly by the anterior tentorial pits (Fig. 6, antp) and laterally by the antennal bases. The clypeus is not separated from the frons by an epistomal suture, but the anterior tentorial pits indicate the anterior limitations of the frons and the posterior limitations of the clypeus. Since there is no trace of a



Figs. 1-8.—1-4. Head of *Ixodiphagus texanus*. 1. Dorsolateral view; 2. Frontal view; 3. Lateral view; 4. Dorsal view. 5-8. Head of *Hunterellus hookeri*. 5. Dorsolateral view; 6. Frontal view; 7. Lateral view; 8. Dorsal view.

clypeolabral suture, the area anterior to the anterior tentorial pits is in reality a fusion of clypeus and labrum. The area bearing one of the compound eyes, one of the lateral ocelli and one of the antennae on either side is the parietal area. The lateral part of the parietals beneath the eyes and antennal bases are the genae (Fig. 7, ge). The narrow band encircling the compound eyes are the ocular sclerites, and similar bands encircling the antennae are the antennal sclerites.

The postoccipital region cannot be demarcated clearly, since the postoccipital suture is suppressed. The posterior tentorial pits, however, afford some help to demarcate the occipital and postoccipital regions.

The postgenal regions are greatly lengthened antero-posteriorly and the extensions of both the sides have intimately fused to leave no suture. A hypostomal bridge is thus formed between the foramen magnum and the bases of the labium and maxillae. The tentorium is seen as a transverse bar through the foramen magnum.

The three ocelli form an isosceles triangle with the anterior median ocellus. The apical or anterior angle is a right angle. The distance between the two posterior ocelli is greater than the distance between the median ocellus and either of the lateral ocelli. The distance between a lateral ocellus and the margin of the compound eye of the same side is slightly greater than the diameter of the ocellus. The fronto-vertex is slightly less than two times as broad as long.

The frontoclypeal area of the head, when viewed from the side, seems to make a sharp angle with the vertical (Fig. 6). The shape of the eye is subovate with the narrower end directed posterodorsally (Fig. 7). The antennae are inserted at the same level as the lower margins of the eyes.

HEAD APPENDAGES

Antennae.—In the female of *H. hookeri* the antennae are eleven-segmented, elbowed, and clavate. The scape is the largest segment of the antenna (Fig. 14). It is about 2½ to 3 times as long as broad and has a distinct flange-like expansion on its lower side. The pedicel makes a sharp angle with the scape thus forming the bend of the elbow. The pedicel is the longest segment of the funicle which consists of six segments (Fig. 14). The last three segments of the antenna form the club (Fig. 14) which is slightly broader than the segments of the funicle.

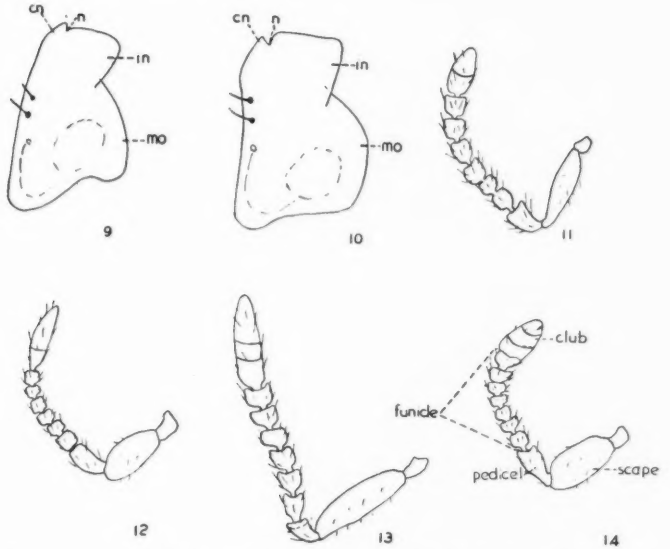
In the male the antenna (Fig. 12) consists of only ten segments and is filiform. The scape, pedicel, and funicle resemble the corresponding parts of the female antenna; but instead of a broad club, as in the female, the antenna of the male terminates in a two-segmented club which is the same width as other segments of the funicle.

Mandibles.—Roughly speaking, the mandible of *H. hookeri* (Fig. 10) is shaped like a quadrilateral with rounded 'angles' and with the proximal and distal sides being almost straight. The inner side is very convex over the posterior half of its course. This convexity forms the molar area (mo). This side then curves sharply on itself making an angle of 90° and this forms the incisor area (in) which is completed by the distal side of the mandible. The distal side of the mandible has a small notch (n) dividing it into an outer small tooth (on), "the canine tooth of Howard, 1907," and a large tooth or the incisor area (in) "the chisel-shaped tooth of Howard, 1907." (Howard applies both these terms to the mandible of *I. texanus*).

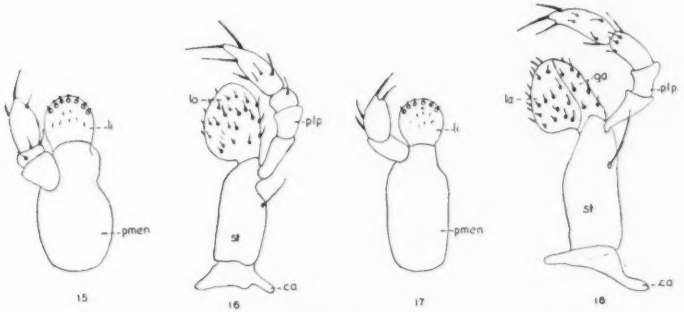
The mandible articulates anteriorly by means of a knob on the lateral angle of the clypeus and posteriorly by a socket on the lower edge of the postgena.

Maxillae.—The maxillae of *H. hookeri* (Fig. 18) exhibit the typical maxillary structure. The cardo (ca) is roughly triangular with its apex directed mesally. The stipes (st) is rectangular in shape, the long axis being in the anteroposterior direction. Distally it bears the palpus (plp) and a much rounded lobe. This lobe, in all probability, represents fused galea and lacinia; it shows a faint suture running anteroposteriorly dividing it into an elongated galea-like structure (ga) and a semicircular lobe (la) which may be the lacinia.

The maxillary palpi (Fig. 20) are four-segmented, with the segments being subequal in size; the relative size and shape of segments is shown in Fig. 20. The first three segments are almost equal to one another in size and in width, each of the segments being longer than broad. Segment four is slightly longer than the rest. Segments three and four are beset with numerous hairs. Segment four always has a terminal hair (Fig. 20) which is slightly longer and stouter than the rest of the hairs. Abnormalities in the segmentation of maxillary palpi sometimes occur and in a few specimens one may find only three-segmented palpi. In general shape and size these palpi resemble a normal palpus and it seems apparent that the third and the fourth segments have fused together. Specimens also occur in which the maxillary palpus of one side is four-segmented while its counterpart on the other side is only three-segmented.

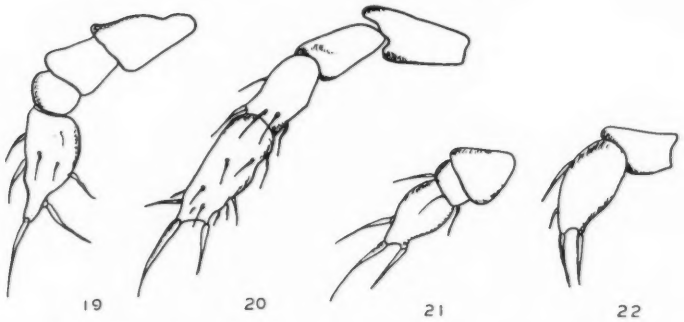


Figs. 9-14.—9, 10. Right mandibles. 9. *I texanus;* 10. *H. hookeri.* 11-14. antenna 11. *I. texanus,* ♂; 12. *H. hookeri,* ♂; 13. *I. texanus,* ♀; 14. *H. hookeri,* ♀.

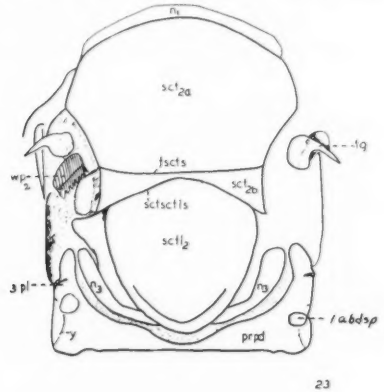


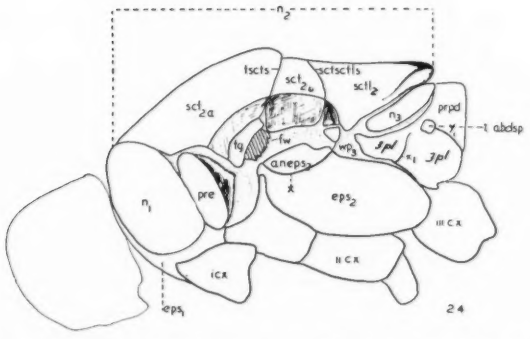
Figs. 15-18.—15, 16. *I. texanus.* 15. Labium; 16. Maxilla.
17-18. *H. hookeri.* 17. Labium; 18. Maxilla.

The *labium* in *H. hookeri* (Fig. 17) consists of a very faintly sclerotized submentum which is square in shape, a large, rectangular, comparatively heavily sclerotized prementum (pmen) bearing the ligula (li) and the palpi. The ligula is a single, rounded lobe beset with hairs. The labial palpi (Fig. 22) are two-segmented; the second segment is the stouter, oval in shape and beset with a few hairs.



Figs. 19-22.—19, 20. Maxillary palpus. 19. *I. texanus*; 20. *H. hookeri*. 21, 22. Labial palpus. 21. *I. texanus*; 22. *H. hookeri*.





Figs. 23, 24.—Thorax of *H. hookeri*. 23. Dorsal view; 24. Lateral view.

CERVIX

The membranous area between the head and the thorax forms the cervix. Cervical sclerites are absent; the head articulates on either side with the occipital processes of the propleuron.

THORAX

The thorax of *H. hookeri*, like the thorax of other higher Hymenoptera, is highly specialized. The apparent thorax (Figs. 23 and 24) consists of the usual three segments plus the first abdominal segment (prpd) which is intimately fused with it.

The pronotum is so closely associated with the mesothorax that it appears as if it were the prescutum of the mesothorax, although the mesoprescutum is absent in this species. The pronotum together with the mesothorax, metathorax, and the first abdominal segment or propodeum, forms a compact capsule supporting the mid and the hind legs and the two pairs of wings. The lateral and ventral parts of the prothorax are, on the other hand, joined loosely by membranes to the anterior end of the thorax and they constitute a suspensorium for the prothoracic legs. The first abdominal spiracles (abdsp) lie just dorsal to the junction of the propodeum with the metepisternum.

THORACIC TERGA

The pronotum (Figs. 23 and 24, n_1) is collar-like in shape, dissociated from the rest of the prothorax and attached to the anterior end of the mesotergum. It is narrowest in the mid-dorsal region, broadening gradually as it arches laterally. The lateral ends of the pronotum lie between the prothoracic episternum (Fig. 24, eps_1) and the prepectus (pre), slightly overlapping both. The protergite shows no signs of demarcation whatsoever.

The mesonotum (Fig. 24, n_2) consists of three parts—scutum (Figs. 23 and 24, sct_2a and b), scutellum ($sctl_2$) and postscutellum. The scutum (sct_2a and b) is divided by a transcutal suture (tscts) into an anterior large plate (sct_2a) which is roughly hexagonal in shape; it is collared anteriorly by the prothoracic notum and separated from the rest of the mesonotum by the transcutal suture. The posterior plate of the scutum (sct_2b) is a comparatively smaller transverse plate, narrow in the middle and broadening out laterally. Just anterior to the lateral ends of this suture (tscts) the scutum bears an anterior notal wing process on either side (usually concealed by the tegula), while the posterior notal wing processes are situated on the edges of the posterior plate, which lies posterior to the transcutal suture. The scutellum is subtriangular in shape. The broadly rounded apex points posteriorly and the broadly convex base anteriorly. The scutellum is limited anteriorly by the scutoscutellar suture (sctsctls). The mesothoracic postnotum is completely concealed under the mesoscutellum which covers it dorsally. On the removal of the scutellum however, it is visible as a narrow transverse plate. It bears a postphragma which extends posteriorly to the second abdominal segment. The posterior end of the phragma is notched.

The metanotum (Figs. 23 and 24, n_3) is a small rectangular plate running parallel to the propodeum posteriorly and overlapped by the mesoscutellum

($sctl_2$) anteriorly; laterally it articulates with the metapeluron (3pl) on either side.

The propodeum (prpd) appears as if it were the last thoracic segment, though, as already mentioned, it is, in reality, the first abdominal segment that has shifted to the thorax. It runs parallel with the metanotum and is separated from it by a membrane. It is connected laterally with the metapleuron. The suture (y) between the propodeum and metapleuron is incomplete. Just before its connection with the third pleuron, the propodeum bears the first abdominal spiracle (I abdsp).

THORACIC PLEURITES

The propleuron (Fig. 24, eps_1) consists of a single triangular sclerite (eps_1) on either side, which in all probability is the proepisternum. On its anterior end this sclerite has a small process which Snodgrass (1910) calls the occipital process of the propleuron, in the case of Hymenoptera. The head articulates with this process of the proepisternum.

As mentioned above, the propleuron consists of a single sclerite on either side. This sclerite does not show any signs of demarcation into an episternum and an epimeron. That this single sclerite is in all probability the thoracic episternum is indicated by a study of the comparative morphology of the prothoracic pleurites in the Order Hymenoptera. The studies of Snodgrass (1910) on the thorax of the Hymenoptera show a gradual reduction in the size of epimeron from lower to higher members in the series and finally in the higher Hymenoptera the entire propleuron consists of a single plate, the proepisternum.

Thus, according to Snodgrass (1910) the propleuron is divided into an episternum and epimeron by a distinct pleural suture in the case of *Arge* species (Tenthredinidae); both the episternum and epimeron are well developed and are as distinct as in any other segment in the above case. *Lygaenematus erichsonii* of the same family also possesses a comparatively large epimeron; while in the case of *Trischiosoma lanuginosa* (Tenthredinidae) the propleuron consists of a single plate, the proepisternum. In the case of *Tremex*, the propleuron consists of episternal plate alone.

In the propleuron of Hymenoptera are, therefore, found distinct proepimeron and proepisternum in lower members of the Order, but as we go higher in the series, the epimeron gradually decreases in size and finally in the higher members, the propleuron consists of a single plate alone. A comparative study thus points to the probability that the single propleural plate is the proepisternum. This condition is also characteristic of other thoracic pleura as well.

The mesopleuron presents some interesting features. The pleural suture is absent; the large episternum (Fig. 24, eps_2) is divided by the anepisternal suture (x), into an upper comparatively much smaller region, the anepisternum ($aneps_2$) and a lower and much larger region, the katepisternum (eps_2). Anterodorsally the episternum bears the wing process (wp_2). Anterior and dorsal to the wing process of the mesepisternum is a shell-like lobe, the tegula

(tg), which overlaps the base of the forewing (fw). Anterior to all these sclerites on either side is the prepectus (pre).

The metapleural episternum is connected dorsally with the propodeum; the suture (y) between these two sclerites is incomplete. The episternum is divided by an incomplete suture (x_1) into an anterior (3pl) and a posterior portion (3pl). The tip of the anterior beak-like portion forms the wing process (wp_3) which gives support to the hind wing.

THORACIC STERNITES

The prosternum consists of a plate lying between the front coxae and behind the ventral part of the episterna. The prosternum is divided by a median suture running along the anteroposterior direction into two right angled triangular plates with their apices pointing posteriorly. From these apices arises the furca of the prothorax. The furca curves sharply anterodorsally.

The mesosternum consists of a single plate extending between the episterna of the mesopleuron. Along the midventral line of the plate is a ridge which apparently divides the mesosternal plate into two equal halves. At the posterior end the sternum bears the furca of the mesothorax.

The metasternum, like that of the mesothorax, is a single plate extending between the metapleurites. In the mid-ventral line it bears a longitudinal ridge.

ARTICULATION OF THE WINGS

The forewing (Fig. 29) is hinged at its base to the anterior (anp) and posterior (pnp) notal processes. Ventrally the wing is supported by the wing process of the episternum. At the anterior articulation of the wing and overlapping its base is a comparatively large tegula (Fig. 23, tg). There are three wing sclerites (ax_1, ax_2, and ax_3). At the anterior margin of the wing near its base is a large plate, the humeral plate (hp). The hind wing resembles the forewing in articulation.

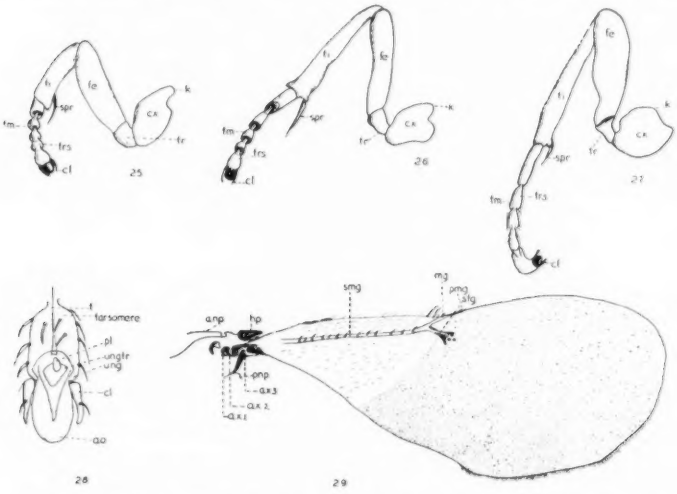
WING VENATION

Only the anterior pair of wings has a well-defined venation. The wing venation in both species is exactly alike. The wing venation conforms to that typical of the Superfamily Chalcidoidea. Running parallel with the anterior margin of the wing is the submarginal vein (smg) which is formed by the union of subcosta, radius and media. This vein joins the marginal vein (mg), which vein is formed by the union of a part of the second part of the subcosta and first abcissa of radius one. Distal to this vein and in continuation with it is the postmarginal vein (pmg) formed by the union of a part of the second part (or abcissa) of subcosta and radius one. Traversing the wing laterally from the junction of these veins is the stigmal or the radial cross vein (stg).

The angle formed by the stigmal and postmarginal veins is approximately 45°.

LEGS

Each leg (Figs. 25, 26, 27) consists of a comparatively broad coxa (cx), and undivided trochanter (tr), a long and stout femur (fe), a spurred tibia (ti), and a five-segmented tarsus trs) terminated by a pretarsal claw (cl).



Figs. 25-29.—*H. hookeri.* 25. Fore leg; 26. Mid leg; 27. Hind leg; 28. Last tarsomere and pretarsus of the fore leg; 29. Right forewing and wing sclerite.

Each pair of legs, however, differs from the others in size and in the shape of the various parts. The prothoracic pair of legs (Fig. 25) is the shortest. The metathoracic pair (Fig. 27) is medium sized, and the mesothoracic pair (Fig. 26) is the longest.

The coxae (Figs. 25, 26, and 27, cx) differ in all the legs. The coxa (Fig. 25, cx) of the prothoracic leg is almost as broad as long, bearing a knob (k) on its dorsal side for articulation with the proepisternum. The coxa of the mesothoracic leg (Fig. 26, cx) is more or less rectangular in shape, being longer than broad. On its proximal surface it has a dorsal knob (k) for articulation with the mesoepisternum and in the middle of the same surface it has a socket in which fits a small knob of the mesosternum. The coxa of the metathoracic leg (Fig. 27, cx) is slightly broader than long; on the dorsal side of its proximal surface it bears a knob (k), smaller than the corresponding knob on the first coxa. This knob articulates with the metaepisternum.

The femur of the foreleg is comparatively broader than those of the other two legs. The ratios between the length and the width of the femur is different in each leg. This ratio in the foreleg is 3 or slightly more; while in the mid leg it is about 5 and in the hind leg it is about 4.

In the tibia of the foreleg (Fig. 25, ti) the ratio between length and

width is slightly greater than 4, whereas in the mid and hind pairs of legs it is 5 or more. Each tibia bears a spur (Figs. 25, 26 and 27, spr). The spurs on the tibiae of the fore and mid legs are about equally stout, while the corresponding spur on the tibiae of the hind legs is slightly more slender. The spur on the fore tibiae arises slightly proximal to the distal end. The spurs on mid and hind tibiae, on the other hand, arise at the distal ends of the tibiae.

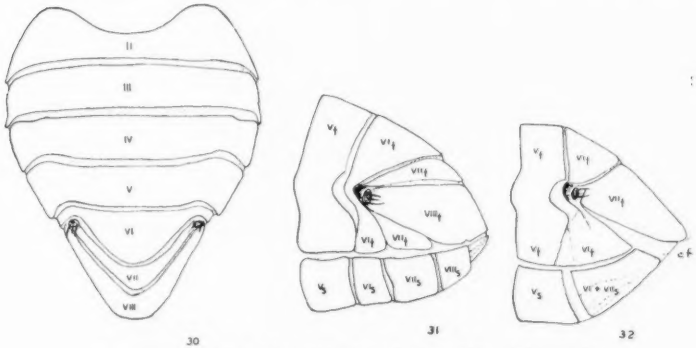
The tarsi (Figs. 25, 26, and 27, trs) are five-segmented in each leg. The segments or tarsomeres (tm) are all of the same size in the fore pair of legs (Fig. 25). In the mid and hind pairs (Figs. 26 and 27) the first tarsomere is the longest and about twice as long as any of the succeeding ones. The succeeding tarsomeres decrease in length until the fourth. The fifth tarsomere is, however, broader than any of the others and is as long, or sometimes slightly longer, than the second tarsomere.

The pretarsus (Fig. 28) is of the same basic structure in each leg. It consists of two lateral claws (cl). Each claw is proximally articulated to the distal end of the fifth tarsomere or the unguifer (ung). In between the claws is the lobe-like arolium (ao). On the ventral surface of the pretarsus is a median basal plate, the unguitractor (ungtr). To the dorsal proximal end of this plate is attached the tendon (t) of the depressor muscle of the pretarsus. Distal to this plate there is a triangular sclerite, the planta (pl).

ABDOMEN

The abdomen (Fig. 30) consists of eight visible segments in the male, and seven in the female; but since the first abdominal segment is more closely associated with the thorax than with the abdomen only seven apparent segments are visible in the male abdomen (Fig. 30), whereas in the female six apparent abdominal segments are visible. In general shape, also, the posterior part of the abdomen of the male, in a dorsal view, is much more pointed (tapering) as compared with that of the female.

Preabdomen.—The preabdomen in both the male and the female is



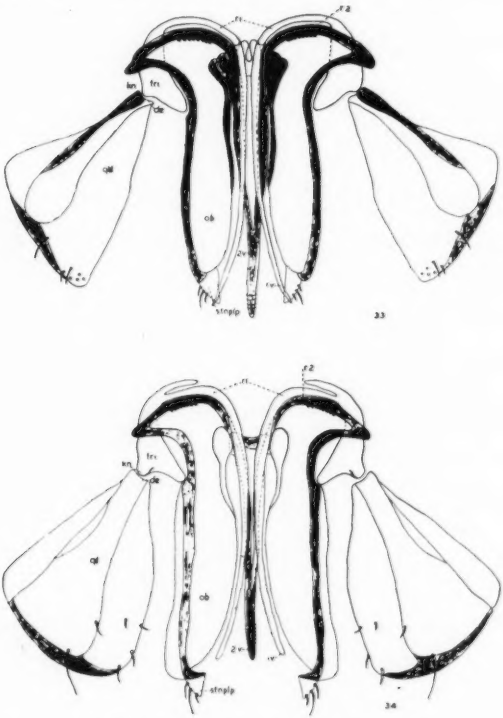
Figs. 30-32.—*H. hookeri.* 30. Dorsal view of the abdomen, ♂; 31. Postabdomen, ♂; 32. Postabdomen, ♀.

alike and consists of four apparent segments (Fig. 30, II, III, IV, and V). As already stated, the first abdominal segment is more closely associated with the thorax than with the abdomen, and hence the first four apparent segments are in reality the second, third, fourth, and fifth segments. In the following discussion the abdominal segments will be numbered, considering the propodeum as the first.

The *tergites* of the preabdominal segments are simple plates extending dorsally and laterally and overlapping the sternites of the corresponding segment. Each one of the tergites of the preabdomen also slightly overlaps the succeeding tergite.

The sternites are simple transverse plates under the corresponding tergites. Laterally the tergites slightly overlap the sternites on either side. The tergites and the sternites thus form a sort of 'ring' for each preabdominal segment. The posterior edge of each 'ring' slightly overlaps the anterior edge of the succeeding ring.

Postabdomen.—The postabdomen of the male and female exhibit considerable differences and therefore will be discussed separately.



Figs. 33, 34. Female genitalia. 33. *H. hookeri;* 34. *I. texanus.*

In the female, the postabdomen consists of the region of the abdomen posterior to the fifth abdominal segment (Fig. 32).

The tergites of these segments appear V-shaped when viewed dorsally. The tergite of the seventh segment (VIIt) in the female is separated from the corresponding sternite, as well as from the lateral part of the preceding tergite by a membranous wedge-shaped cleft (cf). Each arm of this cleft extends anterodorsally on either side of the abdomen to a point where the arms of the V-shaped sixth tergite curve posteroventrally to reach and slightly overlap the corresponding sternite. This membranous cleft is in all probability an adaptation to accommodate the genitalia, which are comparatively large in size and can be easily removed after the abdomen has been torn apart along the membrane of the cleft. The membrane also possibly gives more flexibility to the genital segments.

The sternites of the sixth and seventh segments (Fig. 32, VI + VIIs) are fused to form one transverse plate which supports the genitalia.

Female genitalia.—The female genitalia consist of an ovipositor (a straight tapering shaft (Fig. 33, 2v and 1v) which is made up in the manner normal for Hymenoptera, of the first and second pairs of valves) and several accessory plates.

The first pair of valves lies ventral to the second pair (2v) and each valve of the first pair (1v) can be separated from the shaft, at least partially, while the valves of the second pair (2v) are more firmly joined, perhaps even fused as is sometimes the case in related Hymenoptera. Anteriorly from the base of the ovipositor each of the valves is continued into an elongate, curved ramus valvularum. Each ramus valvularum of the first pair of valves (v1) curves anterolaterally to join a triangular plate (tri) on the corresponding side of the insect. Each ramus valvularum of the second pair of valves (v2) runs parallel to the ramus valvularum of the first valve and joins an oblong plate (ob) apically. There are some nipple-like structures on the concave posterior side of the second ramus valvularum.

The triangular plate (tri) bears three points for articulation, one at each angle: 1) the apical angle is fused with the ramus valvularum of the first valve; 2) the mesal angle bears a small knob-like structure (kn) which articulates with a slight depression in the oblong plate; 3) the outer angle of the triangular plate also bears a similar knob which articulates with a slight depression (de) in a large plate, the quadrate plate (qd).

The oblong plate similarly articulates 1) with the ramus valvularum of the second valve, 2) with the mesal angle of the triangular plate, and 3) with a small knob at the base of the ovipositor. (This knob is, in all probability, a structure of the base of the second valve.) The oblong plate, on its thickened outer margin near the articulation with the triangular plate, bears two small knob-like structures. The oblong plate also bears a small palpus-like structure (stnplp), the sternal palpus, at its distal end.

Homologies of the female genital parts.—Typically the ovipositor consists of three pairs of valves in a generalized insect. The first pair is situated on the eighth sternum, the second and third pairs of valves are borne by the ninth sternum. In higher Hymenoptera, the ovipositor undergoes several modifications but the same basic structure is exhibited by all or most of the

species in this group. A comparative study of the female genitalia by Snodgrass (1925), as well as a study of the development of genitalia in this order by Zander (1900) point out the homologies of the various parts of the female genitalia of Hymenoptera with those of lower insects. Thus, the shaft of the ovipositor in *H. hookeri* which is composed of four rami or valves is made up of the first and second pairs of valves. The ramus which joins the triangular plate is an arm of the first valve. The triangular plate (tri) is the first valvifer (the sternite of the eighth segment). The ramus which joins the oblong plate is an arm of the second valve. The oblong plate (ob) represents the sternum of the ninth segment; it also bears the sternal palpus (stnplp) distally. The sternal palpus is homologous with the third valve. The quadrate plate (qd) represents the tergum of the ninth abdominal segment.

The tergum of the eighth segment is represented in the honeybee (Snodgrass, 1925) by a small plate lying close to the quadrate plate. In *H. hookeri* a plate comparable to the eighth tergum could not be found. It has, probably, been lost phylogenetically.

In the male the postabdomen (Fig. 31) consists of sixth, seventh and eighth segments. The *tergites* (Vt, VIt, VIIt, VIIIt) of these segments are V-shaped. The arms of the sixth and seventh tergites curve posteroventrally to reach and slightly overlap the corresponding sternites. The eighth tergite is a comparatively large V-shaped plate.

The sternites (Vs, VIs, VIIs, VIIIs) are simple, transverse plates lying underneath the corresponding sternites. The wedge-shaped membranous cleft is absent in the male.

The Male Genitalia.—The male genitalia are comparatively very simple and consist of an aedeagus (Fig. 35, ae) surrounded by a tubular phallotheca (pthe). The distal extremity of the aedeagus protrudes slightly out from the phallotheca under normal conditions. The protruding distal extremity of the aedeagus bears small apparently nipple-like structures, the titillators (tit).

IXODIPHAGUS TEXANUS, Howard, 1907

GENERAL EXTERNAL MORPHOLOGY

In general external morphology, *Ixodiphagus texanus* resembles *Hunterellus hookeri*. The chief points of difference in the two species are enumerated below.

HEAD

The head of *I. texanus* is hypognathous (Fig. 1-4), slightly convex dorsally (Fig. 1). It is about three times as wide as it is long. The antennae are inserted at a level which is below the level of the lower margins of the compound eyes (Fig. 2).

The three ocelli form an isosceles triangle (Fig. 4) like that of *H. hookeri* but the apical angle is always obtuse. The distance between the two posterior ocelli is always two or more times the distance between the anterior ocellus and any of the lateral ocelli. The distance between the lateral ocellus and the margin of the eye of the corresponding side is less than the diameter

of the ocellus. The median ocellus in some specimens is slightly larger in size than any of the lateral ocelli.

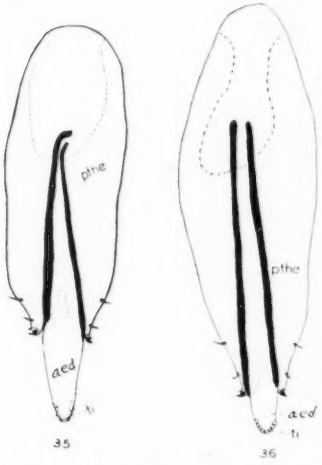
The shape of the eye is elliptical and its longer axis is dorso-ventral.

HEAD APPENDAGES

The antennae of the female of *I. texanus* (Fig. 13) are eleven-segmented and very weakly clavate. The scape is the largest segment of the antenna (Fig. 13) but relative to its length it is much narrower than the scape of *H. hookeri*. It is slightly more than five times as long as it is broad and is only slightly broader than the width of the rest of the segments of the antenna. The flange-like expansion on its lower side is less distinct than in *H. hookeri*. The funiculus resembles that of *H. hookeri*. The last two segments of the antenna form the club which is broader and shorter than the club of *H. hookeri*.

Mandibles (Fig. 9).—The differences between the mandibles of the two species are shown in Figures 9 and 10. The outer side in the mandible of *I. texanus* is slightly convex: (concave in *H. hookeri*).

Maxillae (Fig. 16).—The maxillae of this species differ from those of *H. hookeri* in the shape of the cardo (ca), the maxillary lobe (lo) and the palpus (plp). The difference in the shape of the cardo has been shown in Figures 16 and 18. The faint suture which divides the maxillary lobe into a galea and a lacinia-like structure in *H. hookeri* is fainter or even absent in the lobe of this species. The structure of the maxillary palpi (Fig. 19) is one of the important characters that can be used to distinguish between the two species. Each palpus is four-segmented; segment three is the smallest of all, and it is broader than long. Abnormal palpi like those of *H. hookeri* are found in this species as well.



Figs. 35, 36.—Male genitalia. 35. *H. hookeri*; 36. *I. texanus*.

The labii of the two species have been shown in Figs. 15 and 17, for comparison. The labial palpus in *I. texanus* (Figs. 15 and 21) is three-segmented, while that of *H. hookeri* is two segmented (Figs. 17 and 22). The second segment is the smallest of the three and is broader than long.

THORAX

The thorax of *Ixodiphagus texanus* is slightly convex dorsally, while that of *H. hookeri* is nearly flat. In details of structure it resembles the thorax of *H. hookeri*.

ABDOMEN

The abdomen of the male, as well as the female, resembles; that of *H. hookeri.*

The *female genitalia* of the two species have the same basic structure, but several differences in the shapes of various parts occur (Figs. 33 and 34).

The *male genitalia* show slight differences which have also been figured for comparison (Figs. 35 and 36). In *I. texanus* the protruding distal extremity of the aedeagus is slightly shorter and broader than that of *H. hookeri.*

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LIST OF ABBREVIATIONS

1 abdsp—first abdominal spiracle; aed—aedeagus; anp—anterior notal process; antp—anterior tentorial pit; ao—arolium; ax_1, ax_2 and ax_3—first, second and third axillary sclerites; ca—cardo; cf—cleft; cl—claw; cn—canine tooth of the mandible; cx—coxa; I cx, II cx and III cx—fore, mid and hind coxae; eps_1—episternum of the prothorax; eps_2—episternum of the mesothorax; fe—femur; fr—frons; fw—forewing cut at the base; ga—galea; ge—gena; hp—humeral plate; in—incisor area of the mandible; k—knob of coxa; kn—knob of triangular plate; la—lacinia; li—ligula; lo—maxillary lobe; mg—marginal vein; mo—molar area of the mandible; mxplp—maxillary palpus; n—notch in the mandible; n_1, n_2 and n_3—pronotum, mesonotum and metanotum; ob—oblong plate; oc—ocellus; pl—planata; 3 pl—metapleuron; plp—palpus; pmen—prementum; pmg—postmarginal vein; pnp—posterior notal process; prdp—propodeum; pthe—phallotheca; qd—quadrate plate; r_1—ramus valvularum of the first valve; r_2—ramus valvularum of the second valve; Vs, VIs, VIIs and VIIIs—fifth, sixth, seventh and eighth sternites; sct_{2a}, sct_{2b}—mesoscutum; sctl—scutellum; sctsctls—scutoscutellar suture; smg—submarginal vein; spr—tibial spur; st—stipes; stg—stigmal vein; stnplp—sternal palpus; t—tendon; Vt, VIt, VIIt, and VIIIt—fifth, sixth, seventh and eighth tergites; tg—tegula; ti—tibia; tit—titillators; tm—tarsomere; tr—trochanter; tri—triangular plate; trs—tarsus; tsct—transscutal suture; ung—unguifer; ungtr—unguitractor; 1v—first valve; 2v—second valve; vx—vertex; x—suture dividing the anepisternum and katepisternum; x_1—suture dividing the third pleuron; y—suture between propodeum and third pleuron.

Do Fossorial Rodents Originate Mima-Type Microrelief?

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Dense clusters of small circular mounds or soil pimples are widely scattered on the treeless regions of western United States (Fig. 1). To a climax example of the mounds rising to a height of seven feet on Mima Prairie, Thurston County, Washington, Dalquest and Scheffer (1942) gave the name "Mima mounds." The origin of the mounds was laid to pocket gophers, members of the rodent family Geomyidae Gill, 1872. Later, one of the authors (Scheffer, 1947) extended the hypothesis to cover the "hog-wallow" microrelief of the Central Valley, California, and the pimpled sea-terraces back of San Diego, California. A lively argument has persisted between two groups: those who champion the pocket gopher (Arkley and Brown, 1954; Dalquest and Scheffer, 1942; Koons, 1948; Price, 1949, 1950;

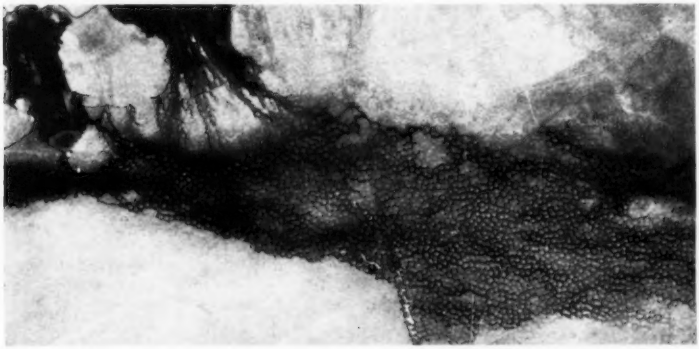

Fig. 1.—Pimple mounds in Albany County, Wyoming, elevation 7,500 feet, 20 miles SW of Laramie, 16 June 1947. Intermound hollows are darkened by a recent flow of irrigation water. Gophers (*Thomomys*) and prairie-dogs (*Cynomys*) living here. Scale 1:45,000. (U. S. Geological Survey.)

Scheffer, 1947; Stallings, 1948), and those who champion the inorganic agencies of earth displacement such as wind, water, and ice (Dietz, 1945; Jackson, 1956; Knechtel, 1952; Melton, 1954; Newcomb, 1952; Péwé, 1948; Ritchie, 1953; Whitney, 1948). Two avenues of research leading toward a solution of the problem are now suggested.

The first is direct experimentation. On the densely timbered northwest coast of the Olympic Peninsula, Wash., there remain a few small prairies, smooth, treeless, and without gophers. Their soil is of glacial outwash identical to that of the mounded, gopher-infested prairies of Thurston County.

As the last ice sheet melted, gophers invaded from the south, and spruce-hemlock-fir invaded from several directions — mainly from alpine forests standing above the ice (Dalquest and Scheffer, 1944). Gophers are unable to live in dense coniferous forest. It is quite clear that the forest occupied the extreme northwestern Olympic Peninsula, with the exception of these relic prairies, before gophers were able to move up from the south. Thus, the present northern limit of distribution of gophers along the Pacific Coast is a few miles north of Mima Prairie and a few miles south of the relic prairies.

As an experiment, then, gophers might be placed on the relic prairies and held under observation for 10 years or more. Would they here — as we believe they did on Mima Prairie — arrange the thin silt-gravel into territorial mounds? Evidence from men (Arkley and Brown, 1954; Koons, 1948) who have watched mounds grow in a lifetime leads us to believe that positive results from the Olympic experiment would appear in a matter of years rather than geologic ages.

A second approach to the problem of Mima-type microrelief is through inquiry of foreign scientists. Since the Geomyidae are confined to a belt running southward from southwest Canada to Central America, the proponements of the gopher theory have assumed that Mima-type microrelief would not be found elsewhere. Following this approach we published an article in Spanish and German (Scheffer, 1954, 1956). The article presented a diagnosis of the Mima-type microrelief, with photographs, and invited communications.

Up to now, only one reply has produced evidence of Mima-type microrelief in a foreign land, and this evidence is open to speculation. Dr. Oliver P. Pearson (University of California) replied on 18 August 1955, enclosing a photograph (Fig. 2) and stating:

> At the northern end of Lake Junin, Department of Pasco, Peru, between 13,500 and 14,000 feet elevation, there is an extensive series of first-class mima mounds, as good as any I have seen in California. Some of the series cover well over a square mile. The first one that I investigated was on an appreciable slope with fairly evenly spaced mounds, varying from 5 to 12 yards apart and 1 to 2 feet high. I camped overnight in the middle of another series of mounds that were slightly larger, but not over 2 feet high, and seemed

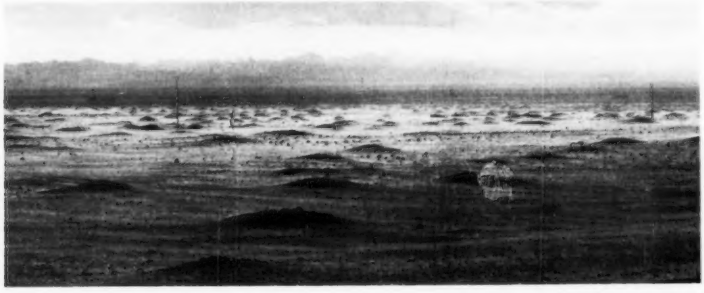

Fig. 2.—Pimple mounds near Ninacaca, Department of Pasco, Peru, elevation 13,500 feet, 16 August 1955. Origin of mounds uncertain; perhaps the work of tucu-tucos (*Ctenomys*). (Oliver P. Pearson.)

to be spaced farther apart. Some of the mound systems are on gentle slopes and some on flat pampa. The vegetation is very short, dry grass and low forbs—nothing higher than 3 inches. The country is grazed by livestock. The mounds seem to have a higher concentration of stones in them than do the surrounding flats. In road cuts, every place a mound system is dissected I saw about 10 inches of stony topsoil underlain sharply by a *very* stony foundation. The foundation is mostly rounded stones with just enough dirt to fill the interstices. No place had mounds that did not show this layering. A few places had layering but no mounds, and between Tinyahuaroo and Huallay was a large pampa with layering and just a trace of mima mounding.

Now as to the zoology; the nearest tucu-tucos (gopher equivalent, family Ctenomyidae) are probably in southern Peru, several hundred miles away. Guinea pigs (ground squirrel equivalent, family Caviidae), have been collected nearby but none lived here. Their droppings are unmistakable and easily seen when present. To be able to send you a careful report on the situation I camped in the midst of a nice series of mounds at Ninacaca. About one out of every 20 mounds had a tunnel opening big enough to accept a man's hand. There were a few tunnels between mounds and numerous tunnels on a nearby, unmounded slope. Scrutiny with binoculars off and on for several hours disclosed no mammals, such as guinea pigs. Spotlighting at night showed neither mammals nor reptiles. I set steel traps and mouse traps in tunnels overnight. The steel traps caught nothing; the mouse traps, one 20-gram mouse (Hesperomys). Fortunately, about one-half inch of good tracking snow fell overnight, so it was easy to determine that at dawn nothing except one mouse had been in or out of about 30 tunnels. I followed a set of mouse tracks for about 50 yards and discovered another Hesperomys in a nest under a 10-inch stone, not near a mound. About 6 AM common birds of the altiplano, the miners (Geositta), started popping in and out of the tunnels. They commonly nest in holes in the ground. I found two bird nests and feathers lying in front of tunnels, probably dug out by hog-nosed skunks.

We have reviewed Dr. Pearson's report in the light of our own observations in Colorado, Wyoming, and South Dakota during 1953-1956. Here both gophers and ground squirrels (family Sciuridae, tribe Marmotini) are widely distributed. And here Mima-type microrelief is common (Fig. 1). It is least obvious — in fact, barely distinguishable when the sun is high — on barren rangelands of the Plains; most obvious on subalpine meadows of the Rockies. It can be seen on aerial photographs in the files of the Forest Service, Bureau of Land Management, and Soil Conservation Service. On certain pimpled plains both gophers and ground squirrels (including prairie dogs) are now living; on others, only one or the other. It is unimportant, so far as the origin of soil pimples is concerned, whether fossorial rodents are absent now from certain places fit for them and within their distributional range. Ground squirrels in general and prairie dogs in particular have been exterminated by poison and disease from vast areas they once occupied before the coming of agriculture. While gophers are rarely poisoned, isolated colonies disappear completely for reasons unknown — perhaps from drouth, flooding, freezing, or disease — leaving only the evidence of their dirt-filled tunnels.

The original theory pointing to the origin of Mima-type microrelief by gophers was developed in the humid Puget Sound Trough where there are no ground squirrels. However, from a study of the distribution and properties of mounds in the semi-arid lands of the West and in Peru it seems necessary to expand the theory to include other species of fossorial rodents as well as gophers. Present evidence points to the gopher as being responsible for the largest pimple mounds. The gopher is, after all, the most completely fossorial of all North American rodents. Next in rank as mound architects are the prairie dogs (genus *Cynomys*) and perhaps certain of the other large ground

squirrels (genus *Citellus*). For the present, the origin of the mounds of Peru cannot be laid to any specific rodent. Mima-type microrelief should be looked for within the ranges of the Spalacidae (eastern Mediterranean), Octodontidae and Ctenomyidae (South America), and Bathyergidae (Africa). Quite possibly there are pimpled areas on the grasslands of Siberia similar to those of western North America. If so, the barrier of the Russian language has kept us from learning about them. Sochava (1944) describes certain frost hummocks of the tundra and mentions cryptically "spotted tundras of other origin."

Our revised theory now describes the Mima-type microrelief as follows: (1) Soil pimples rather evenly spaced, approaching the squeeze pattern one sees in honeycomb cells, and in the territorial distribution of gannets, flamingos, and fur seals on their respective breeding grounds. (2) At times forming irregular rows paralleling the line of a stream, terrace, rock outcrop, or other confining border. (3) On moderately sloping as well as flat terrain. (4) On thin or poorly drained soils only. (5) Generally circular in shape as seen from above, regardless of slope. (6) Built of fine materials in the range of size that rodents can handle (excluding the occasional erratic transported by coyote, badger, or man). (7) Occurring only within the range of fossorial rodents such as the gopher and prairie dog.

Dr. Richard M. Hansen (Colorado Agricultural Experiment Station) has provided in a letter new evidence that, where Mima mounds are gopher-built, each mound tends strongly to remain the territory of a single gopher. On a subalpine meadow of Black Mesa, Colorado, at 9,500 feet, in September, 1955, Hansen saturated a pimpled area with live traps for gophers. He was able to find fresh tunnels on, and to make sets on, most of the mounds; but on only a few of the stony intermound areas. In a week of trapping he took 65 gophers, not counting repeat individuals previously trapped, marked, and released. *On each of 53 mounds he took a single gopher;* on each of 6 mounds, 2 gophers. The single catches included adults and a few subadults, while each of the 6 double catches included an adult female and a subadult. He took no gophers from the intermound areas.

It is quite clear that in this situation individual adult gophers and a few subadults were expressing strong territorial behavior. Because rodents tend to occupy Mima mounds is not, of course, proof that rodents build the mounds. We believe, however, that the similarity between size of territory of rodents on pimpled and on deep unpimpled soils is more than coincidence.

The survival value of Mima mounds to gophers has been discussed and acknowledged by most authors. The mounds have richer vegetation, more friable soil, and better drainage than the intermound hollows. Furthermore, the mounds offer shelter to gophers during cold, wet weather. From recent observations in the highlands of Colorado at time of spring snowmelt we are led to believe that, unless gophers can move to the shelter of mounds or to deep, well-drained soils, they may suffer heavy mortality. On a trip to Black Mesa in early May we were struck by the absence of fresh gopher hillocks on certain unmounded pastures where signs had been abundant the previous fall. Ingles (1949) has pointed out similar effects of snowmelt on gopher populations in the Sierra Nevada.

It is important to recognize that existing Mima-type microrelief is the result of many influences, some aggrading and some degrading in effect. Once a low mound has been established as part of a territorial pattern, its profile will certainly be changed somewhat by the action of vegetation growing more thickly here, acting as a windbreak, catching more snowfall, holding more soil. Where mounds are built on a fairly steep slope, the thin soil of the intermound region may wash downhill, exposing bare rock, bedded gravel, or hardpan. We believe that, where rodents are working continuously they tend to maintain the original circular shape of the mound. Where gophers die off, or are decimated, abandoned mounds may gradually become elongated under the influence of gravity, water, ice, and surface vegetation.

SUMMARY

Studies on the semiarid lands of the Central Rockies and Plains of the United States and on the altiplano of Peru lead to the conclusion that series of low pimple mounds may be formed on thin or poorly drained soils by other fossorial rodents as well as gophers. Where several fossorial rodents occupy the same site, or have recently occupied the same site, it is often difficult to ascribe the territorial pattern of soil pimples to one rodent agency or another. Under all circumstances, the ordinary influences of gravity, wind, water, ice, and vegetation are constantly at work, tending to alter the ideal circular shape of the mounds. Search should be made for Mima-type microrelief in parts of the world other than western United States.

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Primary Productivity in a Dichothermic Lake[1]

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Fayetteville Green Lake is located in Green Lakes State Park near Syracuse, New York. It is the first dichothermic and meromictic lake to have been described in the United States. Its unusual limnological features were first reported by Eggleton (1931) and since that time he has made periodic studies of this lake; his most recent paper on the subject (1956) discusses rather thoroughly the limnology of the lake but makes only meager reference to its plankton population.

Description of the Lake

The lake lies in a short, blind valley that indents the edge of an upland plateau area. The drainage area is relatively small, due to the low rolling nature of the surrounding hills. Green Lake occupies almost all of the valley floor and has a level near that of the floor of the glacial lake plain to the North. The basin is elongate, with the long axis running northeast-southwest (Fig. 1). The surface area of the lake is roughly one-tenth of a square mile and shoreline is approximately 1.6 miles. The maximum depth is 200 feet, as reported by Eggleton (1931), but the extreme northern part is not deeper than 30 feet. This northern end is not typical of most of the lake, as by far the greater length of the shoreline has uniform precipitous contours.

Green Lake's only inlet is from Round Lake, a smaller body of water which has received little study to date. During most of the summer the stream connecting the two is dry. The small watershed has good forest cover of native hardwoods with large plantations of conifers and is made up of 16 soil types. This hilly, forested watershed protects the lake from wind activity especially since the lake shore is fringed by a belt of white cedars.

Floating or emergent vegetation is almost non-existent. Submerged plants are limited in variety to large beds of *Chara*, some water moss and a sparse population of *Potamogeton vaginatus*. Most areas of the lake with less than 50 feet of water have white marl bottoms. Bottom samples from places deeper than this usually contain a fine black ooze with a noticeably greasy feeling and reek with the odor of hydrogen sulfide. The water is colored blue-green, brilliant and quite transparent. The average depth to which one percent of surface light penetrated during the summer of 1955 was 38 feet.

[1] Contribution No. 6 from Dept. of Biology, Western Michigan University.

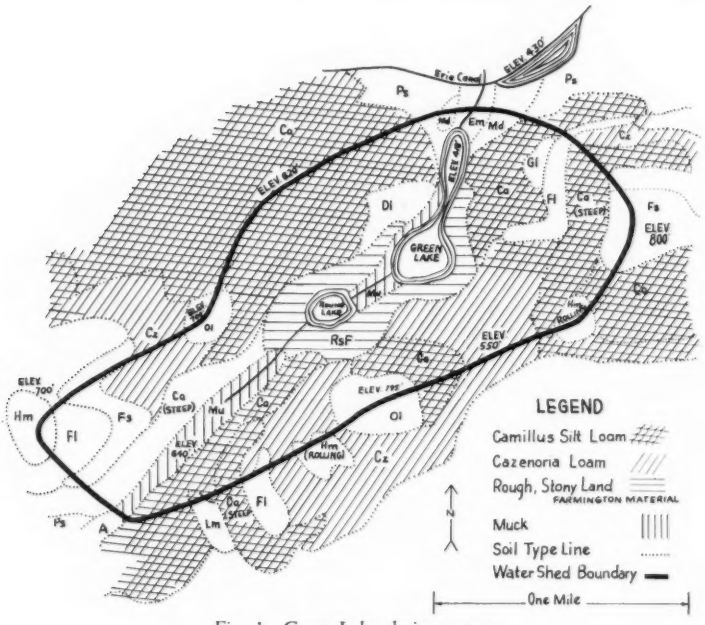

Fig. 1. Green Lake drainage area

INVESTIGATIONAL DESIGN

A review of the surface plankton samplings made routinely over several years at Green Lake reveals several problems, of which one is outstanding. This is the finding that the average ratio between net phytoplankton and zooplankton is 1 to 50,000. Zooplankton were always abundant yet to find even a single cell or fragment of plankton algae was a rare occurrence.

During the summer of 1955 an attempt was made to study this problem. On seven different occasions, two-liter water samples were collected at each of various depths and were centrifuged with a Foerst centrifuge. The organisms are reported volumetrically in cubic microns. Gravimetric determinations also were made and are reported as mg-ash free dry weight per liter. Electrical conductivity was measured by means of a Wheatstone bridge. Dissolved oxygen, free carbon dioxide and total alkalinity were determined according to standard methods and reported as parts per million. These data are included in this paper (Table I), along with the percent light transmission, measured by means of a Beckman spectrophotometer, using distilled water as a blank.

OBSERVATIONS

It may be noted (Table I) that concentration of zooplankton may be found up to a depth of 75 feet. A breakdown of the findings shows Cladocerans

TABLE 1.—Limnological data derived from average of seven samples collected at various times during the summer of 1955 in Fayetteville, Green Lake

	Depth in Feet													
	S	5	10	20	30	40	50	60	65	70	75	80	90	95
Zooplankton	μ^3/liter x 10^5													
Cladocera	15	17	14	11	15	16	14	13	15	17	9	3	0	0
Eucopepoda	19	22	19	18	34	23	27	29	31	53	59	4	1	2
Monogononta	12	15	8	7	6	4	3	2	5	0	0	0	4	1
Plankton Algae	μ^3/liter x 10^8													
	0.0	1.2	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Net Phyto-Zooplankton	Ratio x 10^3													
	1/46	1/53	1/41	1/36	1/55	1/43	1/44	1/44	1/51	1/70	1/68	1/7	1/3	1/3
Light Transmission	Percent of distilled water													
	99		98	98	98.5	98	97.7		98.5	98.5	87	92.5	94	
Specific Conductance	EC x 10^6 at 25° C													
	1090		1200		1290		1310		1400		1700			2100
Ash Free Dry Weight	mg/liter													
	1.41		1.31		1.27		1.41	1.47	1.54	1.45	2.91	1.38		
Dissolved Oxygen	ppm													
	10.3		7.8		7.5		6.3	5.9	5.7	5.3	0	0		
Free Carbon Dioxide	ppm													
	14		10		30		45		51		92	116		
Total Alkalinity	ppm													
	120		129		148		160		193		321	380		410

comprised of *Daphnia longispina*, *Bosmina*, and *Diaphanosomona*. The Eucopepoda were made up mostly of the genus *Diaptomus*, the two most abundant species being *D. stagnalis* and *D. sanguineus*. Some species of *Cyclops* and nauplii were found also. The Monogononta were composed principally of *Conochilus unicornis* and *Keratella*, although other species of

Rotifera were present. It may be noted that plankton algae was nearly non-existent at any depth and the fragmentary pieces that were found were primarily *Scenedesmus*, *Pediastrum* and *Navicula*. The prevailing ratio was one to 50,000.

It was noted that the water samples from 75-foot depths showed peculiar physical and chemical properties when compared with water from other depths. When water samples from various depths were compared in a spectrophotometer the percent light transmission was nearly consistent throughout until the 75-foot layer was reached. At this point it fell from 98.5 (70 feet) to 87. A visual comparison of the water at 75 feet with that from other depths shows the 75-foot layer to be a definite pink.

Chemical factors associated with the sample of water from the 75-foot stratum compared with water from the 70-foot depth show an average loss of 5.3 ppm oxygen, an average increase of 128 ppm total alkalinity, an increase of 41 ppm free carbon dioxide and the pronounced evidence of hydrogen sulfide. Upon microscopic examination, the water was found to be teeming with purple sulfur bacteria. The taxonomic status of this group is still in doubt, but this organism was reported by Eggleton (1956) as *Lamprocystis roseopersicina*.

INVESTIGATION OF PRIMARY PRODUCTIVITY

Since the purple bacteria were obviously an essential factor in primary productivity of Green Lake, a more intensive method of investigation was devised, using millipore filter membranes. These membranes are made of cellulose acetate, are ashless and have a weight reproducible to ± 0.2 mg. The concentration of purple bacteria at various depths was estimated by putting a liter of water through No. 20 silk bolting cloth and then drawing the filtrate through the millipore filter under vacuum. The residues from the silk bolting cloth and the millipore filter were gravimetrically determined and are reported (Table II) as ash free dry weight.

For the first 70 feet of water, 98 percent of the suspended material was retained by the silk bolting cloth while at the 75-foot level, only 46 percent of the suspended material was retained. The purpose of using the silk bolting cloth was to separate the zooplankton from the purple bacteria, which, of course, were not retained by this size mesh. The purple bacteria were collected on the millipore filter, the pore size of which was 0.45 micron. It appears that the low transparency at the 75-foot water level was primarily attributable to the bacterial population.

It may be noted from Table III that the percent light transmission for the water at the 75-foot level was always significantly different than that for water from any other depth. However, there is less difference between the 75 and 80-foot samples than between those from 70 and 75 feet. This would seem to indicate that the maximum population of purple bacteria was located at the 75-foot level.

TABLE II.—Average mg/liter ash free dry weight of suspended material from seven samples of lake water collected at various times during the summer of 1955 in Fayetteville, Green Lake

Depth in Feet	Total Weight of Suspended Material	Retained Wt. Silk Bolting Cloth No. 20	Retained Wt. Millipore Filter	Percent Not Retained by No. 20 mesh cloth
S	1.41	1.38	.03	2.1
65	1.54	1.52	.02	1.3
70	1.45	1.41	.04	2.7
75	2.91	1.35	1.56	54.1
80	1.38	.89	.49	36.0
85	1.09	.72	.37	33.8

TABLE III.—Percent light transmission of waters from various depths in Fayetteville, Green Lake, during the summer of 1955. (Distilled water used as blank).

Depth in feet	Sampling Dates						
	6-19	6-25	7-4	7-22	7-26	8-4	8-17
surface	99	99	99	99	99	99	99
65	99	98	98	98	99	99	99
70	98	98	98	98	98	99	99
75	82	84	80	76	83	85	82
80	92	87	89	82	90	90	90
90	95	92	92	91	98	98	98

NUTRITION DYNAMICS

Since only a few planktonic algae were ever found and a large zooplankton population was observed at every depth down to 75 feet, it would suggest that the primary food source is the purple bacteria. Many of the *Diaptomus* found at various depths contained large amounts of red material, presumably purple bacteria, in their digestive tracts. This supports Bicknell and Bunt's (1952) observation in Sodon Lake that the chief food of the copepod population was the bacterial flora. Since the purple bacteria in Green Lake were limited to the 75-foot level (± 5 feet), the zooplankton would have to travel to this depth to obtain food. This is quite a trip for such small organisms! One may speculate as to whether the carnivores in the zooplankton population lie in wait at the 50-foot level for the well-fed herbivores on their way to the surface.

PHYTOPLANKTON PHOTOSYNTHESIS

One of the other many unexplained questions concerning Green Lake is why are there no planktonic algae. Free carbon dioxide is abundant, temperature conditions are favorable, light is more than adequate. One of the attempts to understand the phytoplankton problem was made through collection of phytoplankton communities in New York State representing four different classes of algae, each class from a different lake. These were the Cyanophyta from Lake Neatahwanta, represented by *Aphanizomenon* and *Polycystis;* the Chrysophyta, collected in Cross Lake, consisting of an *Asterionella-Fragilaria* community; the Chlorophyta, secured from Otisco Lake, one of the Finger Lakes, represented by *Pediastrum* and *Scenedesmus;* and the Pyrrhophyta from Jamesville Reservoir, a *Ceratium-Dinobryon* community. Two aliquots of each of the plankton concentrations were placed in vials, one vial containing 40 ml filtered water from Green Lake, the other vial holding filtered water from the lake where the phytoplankton were collected. A set of each of these was kept at a constant temperature of 15°, 20° 25°C for 3 hours. Sets were run in duplicate (four vials each). Photosynthetic rates were determined by the observed change in pH (a method devised by Verduin, 1951, and used under normal conditions by Jackson and McFadden, 1954). The results of these tests (Table IV) show that the photosynthetic rates of any class of phytoplankton community were three to four times greater in water from their normal source than in water from Green Lake. This would seem to indicate that some factor is lacking or is prohibiting photosynthesis in Green Lake. As to what this may be, one can only speculate at this time. Perhaps there is a lack of iron, of nitrates or of phosphorus.

TABLE IV.—Photosynthetic rates of phytoplankton communities suspended in their own source water and in water from Fayetteville, Green Lake, expressed in micromoles of $CO_2/10^{10}$ micra cube hour.

	Aphanizomenon Polycystis			*Asterionella Fragilaria*			*Pediastrum Scenedesmus*			*Ceratium Dinobryon*		
	Temperature °C											
	15	20	25	15	20	25	15	20	25	15	20	25
Green Lake	.51	.59	.57									
Lake Neatahwanta	2.41	2.46	2.45									
Green Lake				.58	.60	.61						
Cross Lake				1.90	1.87	1.89						
Green Lake							.64	.70	.72			
Otisco Lake							1.90	1.85	1.79			
Green Lake										.63	.65	.60
Jamesville Reservoir										2.28	2.34	2.27

With Green Lake's small watershed, in which most of the soil is poor, little nutrient material can be added yearly from run-off. Since there is strong evidence from temperature measurements, as demonstrated by Eggleton (1931, 1956) and also by Dence (unpublished data), that no overturn occurs in this lake, there can be little in the way of nutritive salts added from the bottom. Further experimentation is necessary before this problem can be fully evaluated.

SUMMARY

A dichothermic lake near Syracuse, New York, has been described and investigation of its characteristics presented. Planktonic algae are almost non-existent whereas zooplankton are abundant. It has been suggested that the food source for the latter is the purple bacteria found in quantity at the 75-foot level in the lake. Experiment indicates that some factor is either lacking or is proscriptive for the growth of planktonic algae.

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Sex Ratios of Some Minnesota Rodents[1]

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An understanding of the dynamics of a population is best obtained by following all of the activities of the individuals of that population. Since this is normally impossible when working with wild species we must depend upon sampling to obtain data—e.g., sex ratios—from which the structure and status of the population can be estimated. It has been suggested by various workers that such factors as season of the year, age of the animals, and method of collecting may cause the observed sex ratios to deviate from the true sex ratio of the population. The following discussion of these points is based upon data gathered from some of Minnesota's more common native rodents. The collecting was done between 1950 and 1955 on areas adjacent to Basswood Lake in Lake County, Minnesota, and in 1954 and 1955 at the Rosemount Agricultural Experiment Station in Dakota County, Minnesota. The work at Basswood Lake was partially supported by the Quetico-Superior Wilderness Research Center.

During the period of study, data adequate for analysis were gathered from populations of the woodland deer mouse (*Peromyscus maniculatus gracilis*), prairie deer mouse (*P. m. bairdii*), red-backed vole (*Clethrionomys gapperi*), meadow vole (*Microtus pennsylvanicus*), and the jumping mouse (*Zapus hudsonius*). All of the woodland deer mice and red-backed voles and part of the meadow voles and jumping mice were taken from the vicinity of Basswood Lake. The rest of the meadow voles and jumping mice and all of the prairie deer mice were taken at Rosemount.

The collecting on the Basswood Lake mainland was based on lines of 50 traps set singly at 30-foot intervals. On the small islands not less than seven traps were used and these islands were covered to the extent that we felt that traps were available to all of the small mammals present. The traps were baited with peanut butter and were then left set for three days. All of the trapping in this area was carried out between June 21 and July 23. The lines at Rosemount were set with three traps at each of 67 stations. These stations were approximately 15 feet apart. Samples were taken at two week intervals between July 15, 1954 and August 15, 1955. The lines were left set for three days. There was no indication that these two methods of sampling the mainland populations produced significantly different results.

The trapping on the mainland areas produced samples with unknown deviations from that of the population. In contrast we felt that all or nearly all of the woodland deer mice and most of the meadow voles and red-backed voles were removed from the small islands so that the sex ratio of this sample is the same or nearly the same as that of the population.

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These data, when summarized in the usual fashion, show considerable variation from group to group (see Table I). The lowest proportion of

TABLE I.—Sex ratios of small mammals by species

Species	No.	Percent ♂♂
Peromyscus m. bairdii	2147	57.9
Peromyscus m. gracilis	1191	51.1
Clethrionomys gapperi	579	48.3
Microtus pennsylvanicus	1615	53.0
Zapus hudsonius	240	50.0

males, 48.3 percent, was found in the red-backed voles and the highest, 57.9 percent, in the prairie deer mouse. The differences between the prairie deer mouse and the woodland deer mouse amounted to 6.8 percent while the greatest difference among the species is 9.6 percent.

Although it has been shown that there is little or no difference in the ease with which male or female muskrats are captured in the late fall (Beer and Truax, 1950) there appears to be considerable seasonal difference (Marshall, 1937 and Hewitt, 1942). Emlen (*in* Schein, 1950) has shown that in trapping an area to extinction, the sex ratios of the trapped brown rats remained fairly constant throughout the period of operation. Bourlière (1954) states that "some data on the sex ratios of adults is certainly to be found in the literature but most of them are unreliable, the probability of capture being usually not the same for males and females."

The data presented here was based upon three-day trapping periods. When comparing the sex ratios of the samples taken on these three days it was found that there was a general shift in sex ratio from day to day (see Table

TABLE II.—Sex ratios of small mammals by day of trap period

	first day		second day		third day	
	No.	percent ♂♂	No.	percent ♂♂	No.	percent ♂♂
			MAINLAND			
Peromyscus m. bairdii	921	55.5	545	57.6	410	61.2
Peromyscus m. gracilis	445	50.8	214	57.5	154	59.7
Clethrionomys gapperi	111	50.5	66	50.0	40	60.0
Microtus pennsylvanicus[1]	91	39.6	65	41.5	42	52.4
Microtus pennsylvanicus[2]	547	55.8	281	56.6	187	65.2
Zapus hudsonius[1]	87	44.8	52	44.2	50	52.0
			SMALL ISLANDS			
Peromyscus m. gracilis	197	40.1	53	54.7	23	60.9
Clethrionomys gapperi	242	44.6	48	50.0	30	40.0
Microtus pennsylvanicus	95	43.2	54	37.0	47	42.5

[1] collection from Basswood Lake only.

[2] collection from Rosemount.

II). In most cases, and in all cases where 100 or more animals were taken on the second or third day, there was an increase in the proportion of males with time. The differences were as high as 9.4 percent in the larger samples.

The six populations sampled from the mainland areas, both at Basswood Lake and Rosemount, all showed increases in the proportion of males as trapping continued. The woodland deer mouse ratios from small island populations showed trends similar to those found on the mainland while the red-backed vole and meadow vole populations from these islands differed in showing little or no shift in sex ratio with time.

Two factors are probably responsible for the differences observed in the data. These are behavior and ingress. It has been shown that the male has a larger home range than the female in the red-backed vole (Butsch, 1954), white footed mouse (Burt, 1940), meadow vole (Blair, 1940 and Hamilton, 1937) and jumping mouse (Quimby, 1951). It has also been suggested that the activity periods may vary in time and length (Brown, 1953). Animals having larger home ranges could be expected to come in contact with a greater number of traps than those with small home ranges. Thus trapped ratios should be biased in favor of males. However, this is true only if the males travel more than the females or if the traps are left out over a period of time so that a larger area is actually sampled for the males. It is also possible that the males tend to be more "foot-loose" than the females and that they either wander more often from their usual home range or change home ranges more often than the females (Frenzel, 1956). This means that ingress may play an important part in the observed sex ratio.

The data from the small islands has the advantage in that there is no ingress and that the same size area is sampled for both sexes. The data show that the female woodland deer mouse is more vulnerable to trapping than the male when the area sampled is the same for both sexes. The first day of trapping produced but 40.1 percent males as contrasted with 54.7 and 60.9 percent males on the second and third days respectively. It was felt that the small island populations of this species were trapped to extinction or at least so few were left that they would not affect the ratios appreciably (Beer, et al., 1954). The over-ail sex ratio for the woodland deer mouse taken from the small islands was 44.7 percent males. There was a higher proportion of females in the first day of trapping than in the population and more males on subsequent days. The trend is the same as that found on the mainland where the first day's trapping produced a ratio of 50.8 percent and the third day 59.7 percent males. The over-all sex ratio for the mainland sample was 54.2 percent males which is much higher than that found on the islands.

The data from the insular red-backed voles and meadow voles show some variation from day to day but there seemed to be no general trend as was observed on the mainland. The sex ratios of the first and subsequent days were very similar. This is at variance with the observed sex ratio shifts noted on the mainland where the proportion of male meadow voles changed from 39.6 to 52.4 percent, and the red-backed voles where it changed from 50.5 to 60.0 percent.

The question that arises here is whether the ratios for the mainland and islands are comparable or not. The over-all sex ratio for the small islands approaches the actual sex ratio. The sex ratio for the mainland is one which represents a sample. Since it is possible that we are sampling different size areas for males and females and that there appears to be a differential immigration of animals into the area, it seems probable that the sex ratio on the mainland for these cricetid rodents is biased in favor of the males and not directly comparable to the island populations. The first day's trapping would appear to approach best the true sex ratio under these conditions.

The sex ratios of the prairie deer mouse and the meadow vole from Rosemount vary considerably from those of the woodland deer mouse and the meadow vole from Basswood Lake but the trends are the same.

While we do not have island data to use as a yardstick in discussing the sex ratios of the jumping mouse there appears to be a tendency for the day to day trapping pattern to be similar to that of the other forms discussed.

It has been shown that sex ratios of the several age classes of a population of rodents may vary (Beer and Truax, 1950, and Schein, 1950). Since we have little basis for placing a true age on these animals we have used a "physiological age" (Schein, 1950) based upon body length for our comparison of sex ratios. There is little to indicate that there is a difference in the rate of growth between sexes in the forms discussed.

In the four cricetid rodents there appears to be a single pattern of sex ratio development (see Table III). In the smallest (youngest) age classes the sex ratio is consistently in favor of the females. The several species then showed a consistent shift in observed sex ratios from one favoring the females in the juveniles to one strongly favoring the males in the sub-adults. This dominance varied from 58.7 percent in the woodland deer mouse to 72.6 percent in the prairie deer mouse populations. As the animals grow older (larger) there is a tendency for the populations to be composed of larger proportions of females. This reversal varies from a shift of about 10 percent back to an even sex ratio in the older classes of meadow vole to a population

TABLE III.—Sex ratios by body length (age) classes

	50-59 mm		60-69 mm		70-79 mm		80-89 mm		90-99 mm	
	No.	percent ♂♂	No.	percent ♂♂	No.	percent ♂♂	No.	percent ♂♂	No.	percent ♂♂
Peromyscus m. bairdii	2	50.0	77	36.5	666	53.2	986	72.6	368	33.7
Peromyscus m. gracilis	1	100.0	26	38.5	207	43.0	566	58.7	296	44.6
Clethrionomys gapperi	–	–	8	25.0	53	50.9	118	61.0	171	62.6
Microtus pennsylvanicus	2	50	10	40.0	63	55.5	187	48.1	352	56.2
Zapus hudsonius	2	50	15	66.7	66	62.1	98	52.0	49	22.4

TABLE III.—(*continued*)

	100-109 mm		110-119 mm		120-129 mm		130-139 mm	
	No.	percent ♂♂	No.	percent ♂♂	No.	percent ♂♂	No.	percent ♂♂
Peromyscus m. bairdii	19	10.5	—	—	—	—	—	—
Peromyscus m. gracilis	37	24.3	—	—	—	—	—	—
Clethrionomys gapperi	127	32.3	69	20.3	5	40.0	1	0.0
Microtus pennsylvanicus	438	60.3	306	48.0	179	44.1	31	54.9
Zapus hudsonius	—	—	—	—	—	—	—	—

containing only 10 and 25 percent males in the larger deer mice and red-backed voles.

The mechanics of these shifts in sex ratio are not known and it may be that it is more apparent than real. However, the following explanation appears to be reasonable. As the animals grow older the males mature sexually and are also subjected to the population pressures exerted by adults as well as becoming more active than the females. These factors plus their newly enlarged home ranges should then cause the males to appear more frequently in the traps and would produce an observed sex ratio which would be high in favor of the males.

The factor of differential mortality rates also enters and affects the sex ratio of both the population and the sample. It is probable that when the young females mature sexually they not only become more active and are taken in the traps more frequently but also become more vulnerable to predation than the males. Thus, during the period when the females are maturing sexually and the males are not, the population sex ratio is shifting to a higher proportion of males while the sample shows a higher proportion of females than is to be found in the population. When the males begin to mature sexually they increase their traveling and are more antagonistic to others of their own sex than the females. Then, as in the females earlier but much more so, the males show a considerable increase in the sample but also are more vulnerable to mortality factors and are eliminated from the population at a greater rate than are the females (see Table III).

The jumping mouse starts with the highest proportion of males in the smallest size groups. The apparent sex ratio started with about two males per female in the small (young) animals and gradually dropped to about one male to three females in the large (old) animals. This difference may be attributed to the fact that the young jumping mice do not mature sexually until the following year. The sexes then mature at the same time and the mortality rates are either even or working against the males in the several age classes.

The age structure of the population affects the observed sex ratio by differences in behavior patterns, in size of area sampled for the two sexes and in the actual sex ratio by the effects of differential mortality rates.

It has been shown that the structure of breeding muskrat populations is affected by density. The more dense the population the lower the proportion of males (Beer and Truax, 1950). Between 1950 and 1955 certain areas on Basswood Lake were trapped on a comparable basis. The data presented here do not show a correlation between the sex ratios and density as revealed by trap success.

TABLE IV.—Monthly changes in sex ratios of *Microtus pennsylvanicus* and *Peromyscus m. bairdii* taken at Rosemount, Minnesota

Month	*Microtus pennsylvanicus*		*Peromyscus m. bairdii*	
	No.	percent ♂ ♂	No.	percent ♂ ♂
January	58	58.6	49	59.2
February	83	57.8	36	61.1
March	95	53.7	10	50.0
April	68	55.9	115	52.2
May	58	44.8	125	54.4
June	130	53.8	75	54.7
July	87	54.0	165	63.0
August	91	56.0	219	64.8
September	114	60.5	476	57.3
October	96	58.3	370	59.7
November	133	61.7	450	55.6
December	75	52.0	57	47.4

The collections at Rosemount were taken over a period of 13 months and two species were taken in numbers which were large enough to examine for seasonal changes in sex ratio (see Table IV). The results of this examination are not clear-cut but there appears to be a tendency for the observed sex ratios to show the lowest proportion of males in the spring and the highest proportions in the late summer and fall. This is undoubtedly due to the changes in the age structure of the population.

SUMMARY

A total of 5772 small mammals from two areas in Minnesota were trapped and the populations analyzed to determine the sex ratios in these species. It was found that the female deer mouse was more susceptible to trapping than the male while there appeared to be no difference between the sexes in the meadow vole and red-backed vole when trapped on the small islands. Since the males are more active than the females there are two possible interpretations of the increase in the proportion of males with time in the mainland populations. The first is that the females are more vulnerable than the males and the second that there is a higher rate of ingress from outside areas in

the males. The male jumping mouse appears to be more vulnerable to trapping than the female. The observed sex ratios and, presumably, the actual sex ratios change with the age of the group. Males appear to be more vulnerable to predation and accidents than the females. Although there was a shift in sex ratio from year to year there appeared to be little relationship with the population density. There was some seasonal shift of sex ratio with the largest proportion of the males being found in the late summer and fall and the lowest in the spring.

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Notes and Discussion

Occurrence of Both Sexes of the Fresh-water Medusa, Craspedacusta sowerbii Lankester, in the Same Body of Water

Since the discovery of the fresh-water medusa, *Craspedacusta sowerbii*, in London by Lankester (1880) and Allman (1880), all collections, apparently with one exception, have consisted entirely of one sex or the other. Payne (1926) stated that in 1925 he found both sexes in approximately equal numbers in a collection from the Kentucky River at College Hill, Kentucky.

On July 22 and August 4, 1954, the author collected a total of 47 medusae in a pond in Southampton Quarry which is located about 100 yards from Williams' Dam on the James River at Richmond, Virginia. Both sexes were present, but the number of each was not ascertained. In finger bowls containing spring water the medusae produced fertilized eggs which later developed into hydroids. The discovery of both sexes in the Southampton Quarry pond appears to be the second case of such occurrence.

Although a dozen or more trips were made to the Quarry during the summer of 1955, no medusae were seen.

Between June 15 and September 30 of the following summer (1956) fourteen visits to the Quarry resulted in collections totaling 579 medusae. Seven of the collections consisted entirely of females. Of the mixed collections none consisted of more males than females; in five of these the sexes were approximately equal in number, but in the other two the ratio of females to males was 133:5 and 175:1 respectively. Five collections of 165 medusae which were made between August 16 and 28 contained no males at all. This number of specimens was large enough to indicate that males were absent from the Quarry during this period. The fact that none of the medusae shed fertilized eggs in the laboratory seemed almost conclusive evidence of the absence of males. Had males been present in the Quarry pond, which covers a rather small area (0.5-1.0 acre), it would appear likely that spermatozoa would have reached some of the female medusae.

Dejdar (1934) listed seventy-five records of the occurrence of *Craspedacusta*, covering the period between 1880 and 1934. Since Dejdar's paper appeared, the medusa has been reported a number of times from various parts of the world, so that the total number of records must be well over a hundred. Since all of these except two (Payne, 1926; and the present report) relate, so far as can be determined, to the occurrence of one sex or the other in a particular locality, it would seem that sex is determined in the fertilized egg as in *Gonionemus* (Joseph, 1925) and dioecious hydras (Frischholz, 1909), the hydroid developing therefrom being either male or female. If this is true, it follows then that hydroids of both sexes must be present in the Southampton Quarry pond. However, none has been found to date, although no really intensive search has been made.

In addition to the two instances of occurrence of both sexes together, as stated above, Weill (1949) reported that collections made in a tributary of the Garonne River in France in 1929 consisted entirely of female medusae, those made in 1949 entirely of male medusae.

The question of why both sexes are not found associated much more commonly may be closely related to the nature of the agent of dispersal, or possibly to certain physical or chemical factors of the environment. Payne (1924) thought it possible that the hydroids might be introduced into new areas along with water plants, fishes, or mussels to which they might be attached. Thus, depending on the sex of the hydroids, medusae of corresponding sex would be produced. Some of the situations, however, in which medusae have been found, such as borrow pits and wells, would appear to preclude any of these means of dispersal. Conceivably water birds might carry the hydroids in mud on their feet. The hydroid is extremely resistant to adverse conditions and possesses remarkable powers of regeneration (Kuhl, 1947). The medusa, on the other hand, is somewhat delicate, and although down-stream distribution in flowing water is easy to understand, it is difficult to see how the medusa might be introduced into another drainage system on the other side of a divide.—NOLAN E. RICE, *University of Richmond, Richmond, Virginia.*

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